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GAMETOGENESIS AND FERTILIZATION IN ALBUGO.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXIX.

FRANK LINCOLN STEVENS.

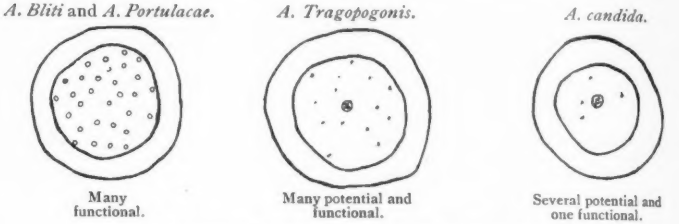
(WITH PLATES I–IV)

[*Continued from p. 98.*]

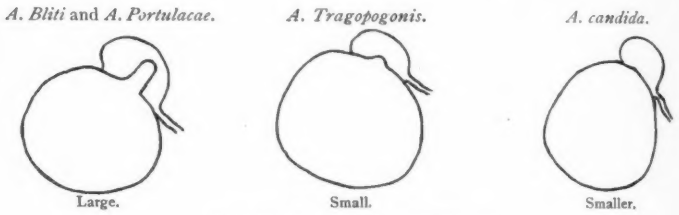
II. PHYLOGENETIC.

THIS study of Albugo has established a series of forms showing advances in certain respects and a marked reduction in others. The species are closely related, and the difference between two consecutive members of the series is not great, although the extremes are widely divergent. There are four prominent structures or conditions connected with the series, namely, the coenocentrum, the receptive papilla, the mode of zonation, and the number of functional nuclei. Arranged in the order of these characters the species may be listed as *A. Portulacae*, *A. Bliti*, *A. Tragopogonis*, and *A. candida*. In this series the coenocentrum constantly increases in complexity of structure and perfection of function, the receptive papilla becomes less conspicuous, the number of functional nuclei decreases, and the mode of zonation varies in the last two species. These conditions are graphically represented in the accompanying figure which is self explanatory. We may consider the series as a possible expression of the phylogeny of the genus. Which conditions are likely to be primitive?

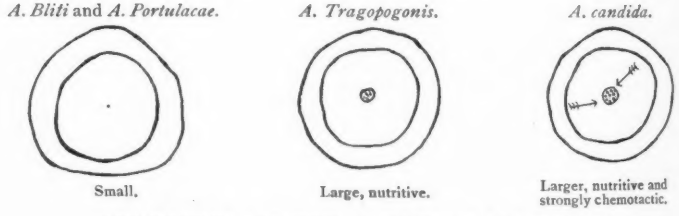
The coenocentrum increases as the receptive papilla decreases; either one or the other must be retrograding. From a study of these two structures alone it might be difficult to determine the true history, but a consideration of the manner in which the



NUMBER OF FUNCTIONAL NUCLEI DIMINISHING



RECEPTIVE PAPILLA DIMINISHING.



COENOCENTRUM ADVANCING IN STRUCTURE AND FUNCTION.

oosphere of *A. Tragopogonis* attains the uninucleate condition shows that this structure in its ontogeny passes through a stage identical with that reached by *A. Portulacae* and *A. Bliti* in their full maturity, thus giving an excellent illustration of the biogenetic law. Both the antheridia and oospheres of *A. Tragopogonis* are multinucleate in their earlier stages, and the development is

strictly comparable to that of *A. Portulacae* and *A. Bliti*, stage for stage. Later the supernumerary oospheric nuclei are eliminated, leaving only one female pronucleus to function. It seems necessary, therefore, to regard the supernumerary oospheric nuclei in this species as potential gameto-nuclei, and to regard the uninucleate condition in *A. Tragopogonis* as due to the suppression of the many and the survival of only one gameto-nucleus. In the light of this behavior *A. Portulacae* must be regarded as the primitive form, and *A. candida* the most highly developed. In view of the great functional importance of the coenocentrum in *A. candida* and *A. Tragopogonis*, it is also rational to regard the coenocentrum as an advancing structure. The reverse is true, however, in reference to the receptive papilla, as there is no indication of its present utility, and everything indicates that it is a vestigial structure. The difference in the mode of zonation between *A. Tragopogonis*, where the protoplasm aggregates into preliminary centers which finally coalesce into one, and *A. candida*, where one central region is formed directly by a recession of the protoplasm from the oogonial wall, may well be regarded as an outcome of the reduction of *A. candida* to a uninucleate condition of the oosphere, and may be taken as further evidence indicative of the highly developed rather than the primitive condition of *A. candida*. It is hardly conceivable that evolution could have proceeded in the reverse direction, that is from the type of oogenesis in *A. candida* to that of *A. Tragopogonis*, *A. Bliti*, and *A. Portulacae*. The serial evidence from the coenocentrum, the receptive papilla, the mode of zonation, and the number of functional nuclei concurs in pointing to the multinucleate conditions shown in *A. Portulacae* and *A. Bliti* as primitive, and the uninucleate oosphere of *A. candida* as derived.

The conditions are almost precisely the same as those in the Fucaceae studied by Oltmanns (1889), with the exception that in Albuginaceae and Peronosporaceae a coenocentrum plays an important rôle in the reduction of the number of functional nuclei to its ultimate expression. It is not difficult to imagine

that the process of evolution of one form from another may have been very rapid after the development of the nutritive region, the coenocentrum. In *A. Portulacae* and *A. Bliti* the struggle between sister gameto-nuclei is possibly close, but the conditions are quite different in forms possessing a highly developed trophoplasmic area in the center of the oosphere, for it becomes a matter of much importance which nucleus is the first to reach and avail itself of the nutrition. The determining factors may be the position of the nucleus, its orientation, or its sensitiveness to chemotactic influences. In any event, a nucleus which gains more nutrition will contribute its substances to a larger fusion nucleus, and consequently leave stronger descendants to the next generation. Moreover, this action of natural selection, aside from furnishing stronger descendants, will foster exactly those characters which enabled the parent nucleus to prevail in the mother oosphere. In short, a condition obtains here which can easily be conceived as one that would conduce to a rapid evolution from a multinucleate to a uninucleate oosphere through the action of natural selection. It is a manifestation of what Klebahn (1899–1900) has termed "Streben nach Einkernigkeit der Sexualzellen," under such conditions that it is possible to recognize the cause of the "tendency."

A peculiarity, probably a consequence, of the uninucleate condition of the oospore of *A. Tragopogonis* and *A. candida* is the division of its fusion nucleus before the spore passes into the winter condition. A series of mitoses rapidly converts the spore from a uninucleate to a multinucleate structure. The division here, as in many of the higher plants, may be regarded as the initial step in germination. In the species with multinucleate oospores no mitoses occur until the long resting period, normally in this case the winter, is passed. In such forms, presumably the primitive ones, the intrasporal evidence of germination appears when the spore ruptures its coat and manifests externally the new activities. It is clear that the inception of division in one case is homologous with that in the other, and in both it constitutes the commencement

of germination. It matters not that in one instance it is before and in the other after the resting period. The divisions which in primitive multinucleate forms come after the resting period have in *A. candida* and *A. Tragopogonis* been transferred to a time before the winter rest. The condition is very similar to that presented in the spermatophytes, where intraseminal germination immediately following fertilization is the rule, although many orchids retain their one-celled condition indefinitely.

Although the division of the fusion nucleus is the first step in germination, the time of this mitosis is subject to variation in different types. The division is delayed in the forms of Albugo having multinucleate oospheres, in *Peronospora parasitica* (Wager 1900), in Saprolegnia and Achlya (Trow 1895 and 1899). The division occurs soon after fusion in species of Albugo having uninucleate oospheres, and in the Peronosporaceae (Berlese 1898). It appears from the consideration of these species that it is not simply a disproportion between the volume of the cytoplasm and the number of nuclei that induces division, for this disproportion is as great in the case of *Peronospora parasitica*, Achlya, and Saprolegnia, as in *A. Tragopogonis*. Wager (1900) has already indicated that in these species, in which the retardation of the fusion is most marked, the inception of division is also most delayed. He says (pp. 275–276):

> *Peronospora parasitica* is at present the only member of the group with retarded nuclear fusion. . . . . In this species it is delayed until the thick zygote membrane has been partly formed. The ripe oospore of *P. parasitica* is uninucleate. . . . . In all the other species of Peronospora which have been examined the ripe zygote is multinucleate.

Similarly, Trow (1895, p. 648, and 1899, p. 175) finds that fusion is slow in Achlya and Saprolegnia, and likewise the division of the fusion nucleus does not occur until after the oospore has passed the resting period. This association of retardation in fusion with delay in division suggests that after the act of fusion is completed, so far as the microscope can give evidence, there may be further changes which the elements of the pronuclei must undergo before fusion is really completed.

The delay of division in species like Saprolegnia, *P. parasitica*, and Spirogyra (Chimelewsky 1888) may be due to a delay on the part of the nuclei in completely preparing for fusion, and to slowness in the act of fusion itself, an act which is not completed when the mere fusion made visible by our present powers of magnification is effected. In this connection Wager (1899, p. 578) makes this suggestion:

> This difference in the behavior of the nucleus during the maturation of the oospore is probably connected with the mode of germination. DeBary has already pointed out that in Cystopus and some other species the oospore on germination produces at once a mass of zoospores. In *Peronospora Valerianellae* and others the oospore at once develops a germ-tube. It may be, therefore, that the uninucleate condition of the zygote indicates germination by a germ-tube, and the multinucleate condition germination by the formation of zoospores.

Apart from the relationships within the group which stand out with more or less clearness, the cytological phenomena emphasize strongly the affinity between the Albuginaceae, Peronosporaceae, and Saprolegniaceae. *Peronospora parasitica*, according to the research of Wager (1900), has a uninucleate oosphere, which is fertilized by the entrance of one antheridial nucleus. In oogenesis the nuclei divide simultaneously while passing to the periphery, as in Albugo, and then one returns to the ooplasm. A highly developed coenocentrum is present, and exerts an attractive influence upon the nuclei even as they lie in the periplasm. All of these conditions, together with the presence of the receptive papilla, clearly attest a relationship between the Albuginaceae and Peronosporaceae. The highly developed coenocentrum and the presence of a uninucleate oosphere indicate that the Peronosporaceae are the more highly developed group. Their ancestors may have been some forms possessing a uninucleate oosphere, similar to that of *A. candida*, from which one of the mitoses has later been suppressed as superfluous. Merely from the evidence of oogenesis, the Peronosporaceae might be regarded as an offshoot from the Albuginaceae after the uninucleate condition had been attained; that is, they may represent a further development of the condition illustrated

in *A. candida*. But certain peculiarities of the asexual organs make such a view improbable. The Albuginaceae and Peronosporaceae may both have attained the uninucleate condition of oosphere independently, each being derived from ancestors having multinucleate oospheres. The probability of the multinucleate condition being the primitive one discredits the validity of Fischer's position (1892, pp. 223, 224) regarding the derivation of the Peronosporaceae and Saprolegniaceae from the Chytridiaceae.

Oogenesis in the Saprolegniaceae resembles that in the Albuginaceae in having a multiplication of nuclei through a mitosis, followed by a degeneration of the superfluous nuclei, thus presenting very closely the condition seen in *A. Tragopogonis*. Trow, Hartog, and Humphrey (1892) failed to report a coenocentrum, but Dangeard (1890) has described a structure in both Saprolegnia and Peronospora which may prove to be the same (*cf.* Wager 1896, pp. 308 and 322).

From my own studies, Pythium closely resembles Albugo in its oogenesis. There is a withdrawal of the protoplasm from the oogonial wall, differentiating a vacuolate periplasm, clearly homologous with that of Albugo. Cytological knowledge of the events of oogenesis in this genus will have great value in determining whether its relationship is closest to the Peronosporaceae or Albuginaceae. The present indications favor the Peronosporaceae, where it was placed by DeBary (1881).

Two diametrically opposed processes of oogenesis occur in the single-egged (eineiig) Albuginaceae and the many-egged (vieleiig) Saprolegniaceae. In the first there is a massing of protoplasm in the center, forming the rudimentary oosphere; in the second a peripheral accumulation of protoplasm leaves the central region comparatively free. There is in Peronospora, however, a movement toward the periphery rather than away from it, resembling in this respect Saprolegniaceae. It is conceivable that Pythium may represent a transitional condition between oogonia with single eggs and those with several, which

would accord with the theory of DeBary that the Saprolegniaceae evolved through the Peronosporaceae.

The origin of the Peronosporaceae and Saprolegniaceae from lower forms is far from clear. Before the discovery of the multinucleate oosphere in *A. Bliti*, a relation to some type like Vaucheria seemed probable. In Vaucheria many nuclei pass into the rudimentary oogonium, after which, as in *A. candida*, the superfluous nuclei retreat from the cytoplasmic region which is destined to become the oosphere. The essential difference is that in Vaucheria the formation of the wall at the base of the oogonium is delayed until the superfluous nuclei pass back into the parent branch. In the Peronosporaceae the wall is formed when the nuclei are still in the oogonium, thus prohibiting their retreat. The result must be either a multinucleate oosphere or a degeneration of superfluous nuclei. Oltmanns (1895, p. 414) has justly remarked that the condition in Vaucheria is very like that in Fucaceae, presenting only such differences as are necessitated by the presence of cell walls between the oogonium and the parent branch. The remark applies with equal force to the Albuginaceae.

The probability that the ancestors of the Peronosporaceae and Saprolegniaceae had multinucleate oospheres removes these groups from Vaucheria-like forms. If there is any relationship the connection must have been at a time in the ancestry of Vaucheria before the abandonment of the multinucleate condition of its oogonium. As Oltmanns (1895) says, the passage of many nuclei into the rudimentary oogonium in Vaucheria is most readily explicable on the assumption that it once produced many gametes instead of the one that is now habitually found, a view that must meet quite general acceptance, as may be seen from the recent paper of Blackman (1900) and the literature there cited.

Mycologists generally acknowledge the close relationship between the Peronosporaceae, Saprolegniaceae, and Mucorineae. The presence of a multinucleate oosphere and antheridium, and the fusion of two multinucleate masses of protoplasm, quite

naturally suggest a possible derivation of the two former groups through the latter. However, as Schröter (1893) has remarked, "Durch das vollständige Fehlen von Schwarmsporenbildung, das oft rein fädige Mycel, die fast nur an der Luft terminal gebildeten Sporen entfernen sich die M. immer weiter von den Algen;" and it is difficult to regard the Mucorineae ancestral to these other Phycomycetes. The manner in which the Mucorineae may have arisen from ancestral algae has been discussed by Davis (1900, p. 308), who has indicated the similarity between the coenogametes of Mucorineae and those of *A. Bliti*. Notwithstanding this similarity it does not seem advisable to regard the Mucorineae as a line productive of such forms as the Peronosporaceae and Saprolegniaceae for the reasons expressed above. The similarity of the vegetative body, however, is sufficient to indicate the possibility, even probability, that the Siphoneae, Mucorineae, Peronosporaceae, and Saprolegniaceae constitute three distinct lines of development from a common parent stock.

Since transition stages in the evolution of these groups are not known, the phylogeny of the coenogamete is little more than a matter for speculation. Two modes of origin are conceivable; either the coenogamete arose from a gametangium producing numerous gametes through the failure of the gametes to separate and become completely individualized; or it may be regarded as a structure, originally multinucleate, which arose and attained sexual differentiation through a line of ancestry composed of multinucleate zoospores.

According to the first view the coenogamete is morphologically a gametangium or physiologically a compound gamete. Each nucleus is the nucleus of a gamete. According to the latter view the coenogamete itself is homologous with a gamete, being a multinucleate gamete. Arguments in support of either view must be based upon such fragmentary evidence as is afforded by the present existing species (which may be made to stand for stages in phylogeny), or the partial repetition of phylogeny through ontogeny. Unfortunately, very little evidence can be

expected from ontogeny, since the conditions prevailing during oogenesis are such that any vestigial attempt to individualize gametes from the nuclei would be at once obliterated. Naturally the individualization of gametes would without doubt become quickly eliminated from ontogeny after fertilization *en masse* became a fixed habit. Perhaps some one of the other eight species of Albugo may exhibit in the oogonium vestigial traces of older conditions and a more perfect individualization of gametes, as the conidia in many Peronosporineae develop zoospores which later merge their individuality into a common mass of protoplasm when the conidium germinates by means of a tube. If the multinucleate sex cells were primitively multinucleate, if there has been an independent line of development starting with multinucleate zoospores and leading through multinucleate isogamous gametes to the coenogamete, it might be expected that some structures indicative of such evolution would now be found among living plants. But there are no stages of such a character known, nor is there any group among the algae or fungi which promises to supply them. Possibly the most suggestive group is the Monoblepharadineae, which has recently been investigated by Lagerheim (1899), who finds only one nucleus in the rudimentary oogonium, and as many nuclei in the antheridium as there are sperms to be formed. There is much evidence, however, to support the hypothesis that the coenogamete is homologous with many gametes, which have failed to separate. This hypothesis postulates an origin from uninucleate, swarming gametes, generally present in coenocytic algae, as Hydrodictyon (Artari 1890), Dasycladus (Berthold 1880), Acetabularia (DeBary and Strasburger 1877), Protosiphon (Klebs 1896), not Botrydium (Rostafinski and Woronin 1877) as is so often erroneously cited,[1] thus showing the prevalence of this mode of sexuality among the algae that are usually looked to for the ancestry of the Phycomycetes. The elongation of the sperm nuclei as they lie in the antheridial tube may also be regarded as indicative of an ancestry in which each nucleus was the

[1] For the most recent work on these species see Iwanoff, 1898.

nucleus of an individual gamete. The fact that Phycomycetes, in conidia and oospores, sometimes lose the ability to individualize their units has an important bearing on the problem. It is well known that the contents of conidia and oospores ordinarily separate into as many regions as there are nuclei, and that these develop into zoospores, each unquestionably an individual. However, if these spores, by a change of external conditions, are induced to germinate by means of a tube, the zoospores do not emerge as individuals. Not merely is there a failure to resolve the protoplasm into individuals, but there is an actual surrender of individuality after it has been attained. Not only does this occur in ontogeny, but it is a very generally accepted belief that it likewise occurred in the phylogeny of this group. In the more primitive forms which germinate by zoospores individualization is not abandoned but is merely delayed, since in germination each fusion nucleus or each of its immediate descendants develops its own plasmoderma and begins independent life. In such form the phenomenon is comparable to delayed wall formation in endosperm, with the remarkable exception that in Albugo fertilization occurs during the period of delay.

Pyronema (Harper 1900) may be regarded as an excellent illustration of a condition in which the individuality of the sexual nuclei habitually finds expression only through their behavior in the act of fertilization. The manner in which the fusion nuclei wander away immediately after fertilization, and the absence of units in the cytoplasm, are strikingly similar to Albugo, as are also the mitoses of the nuclei during oogenesis, the marshaling of the nuclei into a hollow sphere, the participation of the oogonium in the dissolution of the wall adjacent to the antheridium; even the trichogyne resembles in many respects the receptive papilla of Albugo.

While certain Ascomycetes resemble the Florideae more than they do the Phycomycetes, the points of similarity mentioned above between the Phycomycetes, Albugo, and Pyronema, are sufficient to justify careful scrutiny of all features before

abandoning the view held by DeBary (1884) concerning the relationship of these two latter groups. Zoosporangia have not yet been studied cytologically with the completeness they deserve, and it is unwise to deny the possibility of relationship between the ascus and the sporangium until both cell and cilia formation in the Phycomycete zoosporangium is understood.

As the conidia in phylogeny and ontogeny stand for zoosporangia, it is clear that they represent masses of potential zoospores, and are consequently synplasts in the sense in which that word was used by Hanstein (1880). The vegetative coenocyte that develops from the spore is also a synplast, which in phylogeny (and often in ontogeny) goes back to a time when each nucleus governed a definite region of cytoplasm. The multinucleate condition of this vegetative body results from a retardation of cell division, similar to that in the embryo sacs, particularly well illustrated in the gymnosperms, and in the eggs of insects (Hertwig 1892). In the latter forms the delay is not maintained long in ontogeny. Cell division follows soon after nuclear division. In the coenocytic algae there is failure to individualize during a whole generation. Existing forms show that the vegetative body was coenocytic long before the gamete became so. In Albugo, the multinucleate condition of the female sexual cell may be regarded as the result of pushing the synplast habit one step further in ontogeny. The sexual cells were the last to give up their individuality, the vegetative cells the first.

The synplast in the Phycomycetes differs from that of most spermatophytes in many ways, most strikingly, however, in the mobility of its potential units. While it is phylogenetically equivalent to many cells, a compound of potential cells, in the sense that Hertwig (1892) uses the expression, the phycomycete synplast, both in sexual and asexual parts, must be regarded as a morphological unit. The potential units have lost their definite limitations and so their morphological value. Discussion regarding the nature of the vegetative coenocyte may be found in numerous texts, as Strasburger (1880, pp. 372, and 1893), Zimmermann (1896, p. 10), Haberlandt (1896, pp. 12–62),

Verworn (1897, pp. 74–78), Pfeffer (1897, pp. 49–51). It is unnecessary to quote these authors or repeat familiar discussion here, further than to state that they agree in general with the statement of Pfeffer (1897, p. 51), "Auch derartige Erwägungen zwingen dazu, zunächst den veilkernigen Protoplasten als eine morphologische und physiologische Einheit anzusehen."

There is but little in common between the coenogamete, which is a structure of high physiological efficiency, and such structures as have been described by Golenkin (1900) and Klebahn (1899) in Sphaeroplea, which, as Klebahn remarks, resemble cases of polyspermy. They seem to indicate a pathological rather than a normal condition.

The strict maintenance of the individuality of the nuclei and their characteristic behavior in fertilization adds another strong argument to the evidence, which is becoming cumulatively great, that these structures are the bearers of hereditary characters. The apparent ease with which one nucleus can usurp the cytoplasm of many is an argument against the energid theory of Sachs.

[*To be concluded.*]

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A STUDY OF THE SPORANGIA AND GAMETOPHYTES OF SELAGINELLA APUS AND SELAGINELLA RUPESTRIS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXXI.

FLORENCE MAY LYON.

(WITH PLATES V–IX)

[*Concluded from p. 141.*]

GENERAL DISCUSSION.

CONSIDERING the phylogenetic importance of the group, the literature on the Selaginellaceae is surprisingly scanty. More especially is this true of that which treats of the development of spore and gametophyte. Some marked discrepancies in essential features have appeared in these papers, however, and show how much detailed life histories of more species are needed before further inferences are drawn as regards the relation of this group to others. Only one comparatively full account of a single species has yet appeared, Bruchmann's monograph on *S. spinulosa*, published in 1897, although he gives no account whatever of the development of the male gametophyte nor of the sporangia. He had much difficulty in obtaining normal spores,[1] and therefore was unable to follow the earliest stages of the prothallium in detail. In general, however, he agrees with Heinsen and Arnoldi that there is free cell formation within the spore, followed by periclinal and anticlinal cell walls, thus making a disk-shaped mass of cells in the apical portion of the

[1] "Uber die Keimung der Sporen habe ich zu zwei verschiedenen Malen Versuche angestellt. Das erste Mal sate ich sie gleich nach ihrer Reife (im August) auf Torf aus, hielt sie bestandig feucht und schutzte sie im Winter gegen Frost. Die erste Keimung weniger Sporen dieser Aussaat bemerkte ich erst nach zwei Jahren, weitere keimten dann in dritten Jahre, aber der grosste Teil zeigte selbst nach solcher Zeit keine Keimung."

spore. The upper layers of cells are much smaller and irregularly polyhedral in shape. No diaphragm is formed. Three tufts of trichomes grow from the upper surface of the prothallium, rend the exospore into three flaps along the ridges at the apex, and push them up out of the way of the developing archegonia. Only a limited number of the latter develop, some five to ten as compared with Pfeffer's report of thirty in *S. Martensii*. There are four rows of neck cells, with three cells in each row. Pfeffer reports but two cells in each of the four rows in *S. Martensii;* Campbell reports two in *S. Kraussiana*. Heinsen gives a list of eleven species: *S. Martensii*, *S. lepidophylla*, *S. Willdenoviana*, *S. denticulata*, *S. apus*, *S. erythropus*, *S. Helvetica*, *S. serpens*, *S. Douglasii*, *S. glauca*, *S. pilifera*, and says that he agrees with Pfeffer on this point. Bruchmann finds that although several embryos may start to grow, but one comes to maturity. The first division of the oospore of *S. spinulosa* is transverse to the axis of the archegonium, and the cell nearer the neck becomes a suspensor.

The most notable fact, however, is that this embryo has no foot. "Ein Fuss in dem Sinne, sie ihn z. B. *S. Martensii*, *S. Kraussiana* und andere Arten besitzen, fehlt." Whereas, the embryo of *S. apus*, as I have found, has no suspensor. After fertilization the cover cells of the archegonium close together, the walls of the neck cells thicken and turn brown. On the other hand, Pfeffer maintains that the neck of the archegonium of *S. Martensii* gapes widely during the entire embryonic development; and he represents the suspensor pushing up into the neck canal like a wedge. This latter method is the rule in most pteridophytes, and hence *S. spinulosa* together with *S. apus* and *S. rupestris* are exceptions.

In the last twenty years, as far as I know, but four other contributions have been made to a knowledge of these phases of the history of the Selaginellas. In 1871, Pfeffer published his paper "Die Entwickelung des Keimes der Gattung Selaginella." The extreme difficulty of interpreting the spore and prothallial structures, even with the aid of all the modern technique, makes

the description given by this author seem an extraordinary performance, and none the less that apparent discrepancies with other species may disappear upon reexamination. His account of *S. Martensii* differs from the foregoing in the following particulars: The megaspore when about one fourth its final size possesses two coats, exine and intine. Against the inner surface of the latter lies a thick layer of protoplasm inclosing a transparent fluid in which floats a large "nucleus." Near the apex "the protoplasm has a different appearance," but he was unable to interpret it. Obviously, he misinterpreted the so-called nucleus, which is the protoplasmic vesicle, and in all probability the peculiar appearance near the apex was due to the presence of the real nucleus. A dome-shaped diaphragm separates the gametophyte into two regions. This he thinks arises at the first division of the spore into two cells. The one toward the apex of the spore becomes subdivided into a tissue three layers thick in the middle, one layer at the periphery. The continuous division of the lower cell fills the basal portion of the spore with larger cells. The hollow spherical portion of the gametophyte below the disk he describes as becoming filled with "freigebildete Primordialzellen." He could not demonstrate the presence of nuclei in these cells, but regards it as probable. According to his statement, the growth of the prothallium occurs at two periods. The disk-shaped mass of cells appears before the spores are shed, the tissue below the diaphragm, the "secondary endosperm," afterward. Archegonia do not develop until the spores fall.

In 1894 Heinsen reexamined the species studied by Pfeffer. He fell into the same error as regards the interpretation of the protoplasmic vesicle and nucleus in the young megaspore. He was unable to determine the origin of the megaspores, other than that a tetrad arose endogenously in the spore mother cell. He denied the existence of a primary and secondary endosperm, and of a diaphragm, and corrected Pfeffer's misinterpretation of the food balls in the gametophyte cavity "as freely formed cells." Infrequently he found the archegonia formed in unshed spores.

The diaphragm which Pfeffer thought was the wall of the first division of the spore Heinsen regards as the plane of separation between the small cells at the apex of the gametophyte and the larger ones below, and not a wall. He also refutes Pfeffer's statement that ultimately the cell divisions completely occupy the basal region of the spore. Heinsen lays great stress on the supposed fact that the nuclei of the Selaginellaceae increase solely by direct division. He investigated material killed at all hours of the day and night, not only spores but vegetative tips, with special reference to establishing this point. He found a total absence of karyokinetic figures. As this statement, which if true would be most surprising, has not been refuted by later writers, it may be of interest to note a possible explanation of the error. In describing his methods of imbedding, Heinsen says that he killed his material by immersing some specimens for ten minutes in Flemming's fluid, others three minutes in a 1 per cent. corrosive sublimate solution, still others "mit gleich gutem Erfolge wante ich ein zweimaliges schnelles Eintauchen in kochendes Wasser an." It is doubtful whether any of the killing fluids thus employed had opportunity to penetrate the sporangium wall in so brief a contact; in which case his material died a lingering death through the washing and dehydrating processes. Under such conditions naturally there would be no traces of karyokinesis. The statement that he had as good results from two quick dips in boiling water as from the Flemming fluid is otherwise inexplicable. It is somewhat difficult to determine whether Heinsen means his statements to be general with regard to all the species he enumerates or not. His summary leads one to assume that the sequence of events there set down is true of the eleven species above named. There are certainly inaccuracies in many details if applied to *S. apus*.

Arnoldi in the *Botanische Zeitung* of 1896 followed in a brief article on "Die Entwickelung des weiblichen Vorkeimes bei den heterosporen Lycopodiaceen." He investigated *S. cuspidata elongata*, and gives a résumé of Heinsen's paper. He agrees with Heinsen on all points, thus reiterating the misinterpretation of

the spore content. Campbell in his *Mosses and Ferns*, published in 1895, gives an account of his investigation of *S. Kraussiana*. He too describes "the single large globular nucleus" (*i.e.*, the protoplasmic vesicle) of the megaspore. The diaphragm which exists in this species he explains as arising, not as Pfeffer thought from the first division of the spore, but from the thickening of the walls of the lowermost layer of cells of the disk at the spore apex. He finds "numerous small nuclei" scattered through the protoplasm of the spore cavity, and the protoplasmic layer thickens until it "completely fills the cavity of the spore." I have examined *S. Kraussiana* with reference to these points. The diaphragm is very evident and obviously formed in the manner described by Campbell. I can demonstrate no nuclei at any period in the spore cavity, nor any protoplasm. The protoplasm forms a layer next the wall, as in *S. apus*, and the vacuole within is full of food matter, at first a fluid, then an emulsion, and finally filled with granules and small balls of matter which stain like nuclei. The protoplasmic layer grows thicker, but never fully occupies the interior space as Campbell describes.

The latest contribution is that of Fitting (1900), "Bau und Entwickelungsgeschichte der Makrosporen von Isoëtes und Selaginella und ihre Bedeutung fur die Kenntnis des Wachstums pflanzlicher Zellmembranen." He corrects the error made by each of the above named writers in interpreting the parts of the megaspore. An attempt to discover the exact origin of the megaspores failed, due to the fact that the spore mother cell stained so deeply in all his preparations that the details of the evolution of the four spores could not be made out. He was unable to avoid shrinkage of cells. There follows a very detailed account of the development of the spore coats, in which he differs from Heinsen as regards their origin. He drew conclusions largely from living material examined in a salt solution. As I have said before, the interpretation of the origin of the spore coats seems to me largely a matter of theory, and one who has examined the young spores of *S. apus*, while inclosed in the sporangium and surrounded by sterile mother cells, is

skeptical of the results obtained by this method of investigation. He fails to comment on Heinsen's statement with regard to the method of cell division. Both Arnoldi's and Fitting's articles have been comparative studies of certain phases of the Selaginella life history with the same stages of Isoëtes. Thus, until the year 1900 we have not had a correct interpretation even of the parts of the megaspore.

MALE GAMETOPHYTE.—We are indebted to Millardet's memoir for our earliest knowledge of the male gametophyte. This work appeared in 1869, and almost no detail of importance has been added by later workers. In 1885 Belajeff repeated Millardet's work on the same species and corroborated all essential details. There has been no other during the last sixteen years until the present account given in this paper of *S. apus*. How much the discrepancies between the two are due to differences in methods of technique, rather than to specific characteristics, remains to be demonstrated. Millardet and Belajeff both examined the microspores of several species of Selaginella (*S. Kraussiana*, *stolonifera*, and *cuspidata*) in living condition, then added various reagents to the microscope slide, focusing through the spore coats or crushing them by pressure of the cover glass, to determine the phenomena taking place within. The material for the account of the male gametophyte of *S. apus* was killed, imbedded, sectioned, and stained without removing the spores from the strobilus. It will be seen that the main difference lies in the fact that in the earlier accounts there are eight cells described which constitute an antheridial wall; that later these cells disappear, and the sperm cell complex floats free in the cavity thus formed. Both authors state that they were unable to secure a cellulose reaction for the cell walls. On the other hand, I could demonstrate the presence of no such walls in *S. apus*. The first division of the spore results in two free cells. The first, according to Pfeffer's and Millardet's view, is the reduced vegetative part of the prothallium. The latter, which I have called the generative cell, divides at once into a complex of sperm cells. Is it possible that the protoplasmic films surrounding the vacuoles

containing food bodies were mistaken by these authors for cell walls? It is not quite certain that the species of Selaginella called *Kraussiana* in America is the identical one known by that name in Europe. The writer investigated the American form and found the sequence of events identical with those that obtain in *S. apus*. In attempting to repeat the methods employed by Millardet and Belajeff, it was impossible to distinguish through the spore wall the nuclei from the food granules, as both stained alike. Removing the exospore by shoving the cover glass to and fro was a tedious performance, whose results hardly repaid the effort. Moreover, it was impossible to manipulate the stains with enough precision to differentiate the nucleoli. As regards the spermatozoids, explicit statements are few. Belajeff figures those of *S. cuspidata* as biciliate bodies, somewhat elliptical in shape, pointed at the ends, with a slight spiral twist. Millardet gives substantially the same description, but no figures. In connection with his account he makes this reference to the work of M. Roze, who had published his observations in 1864:

> Ainsi qu'on le voit, mes observations sur la forme des anthérozoïdes du *Selaginella Kraussiana* sont loin de s'accorder avec celles de M. Roze sur les anthérozoïdes des *S. Martensii* et *S. Galeottii*. Toutefois, comme il a en affaire à des espèces differentes de celle que j'ai étudiée, je m'abstiens de toute discussion sur ce sujet.

That there existed little information on the subject at this time (1869) is evidenced by the following statement:

> Les seules observations que je connaisse sur la germination des microspores du genre Selaginella sont celles de M. Hofmeister et de M. Roze. Ces deux auteurs se sont bornés à mentionner le fait de la production, dans la spore, de cellules contenant chacune un anthérozoïde. C'est M. Hofmeister qui a constaté le premier l'existence, et la de ces animalcules; M. Roze a montré qu'ils sont biciliés.

So far as I can determine, the authors who have described spermatozoids of named species of Selaginella that they themselves have seen are as follows:

1862. Hofmeister.

1864. Roze first demonstrated two cilia in *S. Martensii* and *S. Galeottii*.

1869. Millardet thus describes the spermatozoids of *S. Kraussiana:*

Il m'a semblé qu'elle se colore en violet par le chlorure de zinc iodé; je n'ose toutefois l'affirmer. On voit en dedans d'elle un filament roulé en hélice, soit à droite, soit à gauche, de façon à faire environ deux tours complets; l'une de ses extrémités est occupée par le granule réfringent d'amidon que je viens de signaler et par suite extrêmement visible; l'autre est à peine distincte. La première constitue la partie postérieure du corps de l'anthérozoïde, elle décrit un cercle plus étroit que le reste de l'animalcule; on voit d'habitude à côté d'elle quelques granulations à peine appréciables. Les cils semblent placés l'un à côté de l'autre; on les distingue difficilement du corps.

. . . . Ces détails serviront à l'intelligence des différentes formes des spermatozoïdes. Dans leur état de développement complet, ils sont entièrement débarrassés de leur vésicule et de la membrane de leur cellule mère, et présentent à l'extrémité postérieure un corpuscule d'amidon; il est resté dans la vésicule où on le retrouve; c'est là une seconde forme. Une troisième est constituée par les animalcules qui portent avec eux une vésicule; une quatrième, par ceux qui ne sont qu'incomplètement dégagés de leur cellule mère.

Dans la forme la plus dévéloppée, le corps est presque droit et décrit une spirale à peine sensible. Sa longueur dans cet état est 0.018 ^{mm} environ. Il s'amincit graduellement depuis l'extrémité postérieure jusqu'à la naissance des cils: son épaisseur maximum ne dépassé pas 0.0007 ^{mm} environ. En avant il se bifurque et se termine ainsi par deux cils très-tenus, deux fois aussi longs le corps.

1871. Pfeffer described the male gametes of *S. Martensii*, and *S. caulescens*.

1885. Belajeff examined *S. cuspidata*, *S laetevirens*, *S. Martensii*, *S. caulescens*, *S. stolonifera*, *S. Kraussiana*, and *S. Poulteri*. Of these he gives figures only of the spermatozoids of *S. stolonifera*.

Thus, in the thirty-nine years since the speramatozoids of the Selaginellaceae were first described, there have been only four contributions upon the subject in which the spermatozoids of but eight species are described from direct observation vouched for by the writer.[3] The difficulty of determining

[3] 1. *S. Martensii:* Roze, 1864; Pfeffer, 1871; Belajeff, 1885.
2. *S. Galeottii:* Roze, 1864.
3. *S. Kraussiana;* Millardet, 1869; Belajeff, 1885.
4. *S. caulescens:* Pfeffer, 1871; Belajeff, 1885.
5. *S. cuspidata:* Belajeff, 1885.
6. *S. laetevirens:* Belajeff, 1885.
7. *S. stolonifera:* Belajeff, 1885.
8. *S. Poulteri:* Belajeff, 1885.

the structure of bodies so extremely small can hardly be overestimated.

With either a Bausch & Lomb $\frac{1}{12}$ oil immersion objective and $\frac{3}{4}$ ocular, or a Zeiss oil immersion 2^{mm} and ocular 3, I was able to make out the spermatozoids only by their characteristic rotary movements as they left the microspore of *S. rupestris*. Their spiral form and attached vesicles were facts determined rather by interpreting appearances by those I had definitely seen in apparently similar but larger bodies, than by actual observations. The spermatozoids of *S. apus* are somewhat larger, and I feel that there is less likelihood of error in describing them. It is obvious that a more critical examination of many species is needed before much weight be placed upon the so-called aberrant forms of the Selaginella spermatozoids in tracing the phylogeny of the group.

THE DEVELOPMENT OF THE SPORANGIA.—The two most recent and important papers on the development of the sporangium are Goebel's (1880) and Bower's (1894). I shall quote verbatim Bower's summary of results from Selaginella:

1. The sporangium is eusporangiate, and arises from the tissue of the axis, above the subtending leaf; the position varies in different species.

2. The origin of the sporangium is similar to that of Lycopodium, and especially resembles *L. inundatum*, to which species the mature sporangium also is similar in form.

3. Two primary archesporial cells are usually present in each radial section, and these are derived, as in *L. inundatum*, from segmentation of two distinct cell-rows; as seen in tangential section, the archesporium is referable to three or four such cell-rows.

4. The first periclinal divisions in these cell-rows do not always define the archesporium finally; subsequent periclinal divisions may result in addition to the central mass, as has been proved for Equisetum; but here the addition is less regular.

5. The tapetum results from tangential division of the outermost cells of the central mass; the greater part of it originates as described by Goebel.

6. The tapetum is thus a sterilized part of the potential sporogenous tissue; a further example of sterilization is seen in the megasporangium, where all the sporogenous cells are disorganized, excepting the one mother cell of the megaspores.

7. Abortive sporangia are to be found at the base of the strobilus as in many species of Lycopodium.

With regard to the derivation of the sporogenous tissue, repeatedly radial sections show a distinct plane of segmentation separating the sporogenous tissue into two such definite regions that it is difficult to avoid the conviction that each complex is the progeny of two independent cells. The term "archesporium" is used by Bower to signify the lower cell or cells. I have used the term to indicate the superficial cell itself. With regard to the fourth statement, my observations on *S. apus* do not agree. With the fifth and sixth statements, as regards the origin of the tapetum, my observations are in accord. The seventh statement I find true of *S. rupestris*, but not of *S. apus*.

In no particular do my preparations agree with Campbell's figures of the sporangial development of *S. Kraussiana*.

Of no little interest is the incomplete septum in the microsporangium of *S. rupestris*, which arises above the pedicel. In vertical section, the resemblance to the celebrated fossil *Lepidodendron Braunii*, as figured by Bower (see his *plate 48, fig. 100*), is very marked. He discusses in the accompanying text the possible function of this region of the sporangium. "Possibly," he says, "these extensions of sterile tissue may have facilitated the nutrition of the developing spores, or they may perchance have contributed to the mechanical support of the sporangial wall." In connection with the former theory, it is noteworthy that this septum is found only in the microsporangium, where some of the spores are remote from the tapetum. A feature that may have some bearing on this point is the fact that the megaspore mother cell, so far as I have observed, is always near the periphery of the sporogenous mass and never at the center, a favorable position to secure nutrition from the tapetum. Scott in his *Studies in fossil botany*, 1900, says, *à propos* of this feature in *Lepidostrobus Veltheimianus*, "this structure may be compared with the trabeculae of Isoëtes. It is best shown in the microsporangium, but may have originally been present in the megasporangia also."

Of even greater interest is the simultaneous discovery of a paleozoic lycopod each of whose sporangia contains a single megaspore or embryo sac, which presumably was fertilized while still attached to the plant, with the condition that I have described above that obtains in *S. rupestris* and *S. apus*. Of the integument that grows up about the sporangium of the *Cardiocarpon anomalum*, described by Scott, leaving at the top an open slit-like micropyle, there is no trace I think, except that in *S. rupestris*, quite late in the development, after the embryo has formed, the megasporangium becomes sunken in a shallow pit formed by the cushion-like upgrowth of the sporophyll around the pedicel. This outgrowth hedges in the ligule with the sporangium, and may be homologous with the Lepidostrobus integument. Scott's statement, therefore, that "the recent discovery of Lepidostrobi with integumented, seed-like sporangia, in which only one megaspore came to perfection, shows that some paleozoic members of the group went far beyond any of the living representatives in the differentiation of their reproductive organs," needs modification in view of the fact that *S. rupestris* normally at the present day produces seed-like sporangia with well developed embryos.

SUMMARY.

1. In both *S. apus* and *S. rupestris* the sporangium frequently, if not always, may be traced to a single superficial cell, the archesporium.

2. The sporogenous tissue may arise in two ways. First (*S. rupestris*), from the single hypodermal cell formed by the archesporium being divided by a periclinal wall, thus producing a wall and a sporogenous cell. Second, by the archesporium (which in this case is assumed to consist of two independent superficial cells) dividing into four cells by a periclinal wall, the two hypodermal cells thus formed developing the sporogenous complex. In each case the epidermal cells form the sporangium wall. It is possible but not demonstrated that the second case may be a phase of the first wherein the original superficial archesporial cell divided by an anticlinal wall.

3. The tapetum is formed in part from the sporogenous cells near the exterior of the mass, and in part from adjacent vegetative cells which come to form a more or less regular layer. It is defined very early, and is active and glandular up to the period that the spores have attained their full size, then becomes reduced to a thin epithelial-like layer lying against the sporangium wall.

4. Microsporangia and megasporangia are indistinguishable before the spore mother cells are differentiated. At this stage, in the case of the megasporangium, one or rarely two cells become more conspicuous and divide into spores. If microspores are to be formed, the majority of the cells continue dividing. After the megaspore mother cell is differentiated, all other cells in the megasporangium cease dividing.

5. In *S. apus* four megaspores arranged tetrahedrally are formed within the spore mother cell. In *S. rupestris* four spores may develop in the same manner, only one or two of which may come to maturity; or, most commonly, there may be but a single division of the mother cell nucleus, in which case there are but two spores formed; or again, there may be a redivision of one only of the two daughter nuclei, resulting in three spores of which only one or two attain maturity. Isolated cases have been met with where but one megaspore was formed. As there were no signs of other aborted spores, presumably the megaspore mother cell never divided, but became directly the single megaspore. In no case have more than two spores in a single megasporangium been found which were fertile, and very frequently only one.

6. The megaspore of each species has three distinct coats, the exospore, mesospore, and endospore. The former originates on the inner face of the spore mother cell membrane, and when first distinguishable is a film of unequal thickness. This either directly or indirectly gives rise to the exospore. A thick layer develops between the exospore and the protoplasmic vesicle, which later in its history separates into two layers, the mesospore and the endospore.

7. The female gametophyte is formed by free cell division of the megaspore, the nuclei dividing by indirect division. These nuclei are confined to the apical portion of the spore. Several layers of nuclei are formed by repeated tangential and radial divisions so that there are six or seven in the apical region and one in the basal. Areas of cells are blocked off by protoplasmic radiations passing from the apex outward and inward. The walls of the cells are produced by nuclear plates in the final division. There is no diaphragm, and at no stage of its development are there nuclei in the lower or the central portions of the gametophyte, which at first contains liquid, and finally a semi-solid mass of granular matter.

8. A cushion of cells protrudes through the tripartite cleft in the exospore at the apex. From cells in the upper row of this cushion a limited number of archegonia develop. The cells of this region are markedly smaller than those in the other regions of the gametophyte. No part of the archegonium protrudes from the general level except the cover cells.

9. The megaspores and gametophytes are nourished by matter secreted by the tapetum and passed through the spore mother cell membrane, which persists until the spores are nearly half grown.

10. The microspores develop in a fashion analogous to the megaspore. A large percentage of the mother cells form tetrads, the largest proportion of which are aborted at this stage.

11. The male gametophyte of *S. apus* consists of a single prothallial cell and an ovoid naked mass of potential sperm cells arranged in two groups. There is no antheridium, nor is there a wall which separates the prothallial from the sperm cells.

12. The spermatozoid of *S. apus* is a spirally coiled body; that of *S. rupestris* is of similar shape but much smaller. The presence of cilia in either was not demonstrated.

13. The megasporangia and microsporangia of both species open by definite lines of dehiscence.

14. Fertilization in both species occurs while the spores are

unshed and the sporangia are still attached to the strobilus. At this period the strobilus ceases to form new sporangia. The strobilus of *S. rupestris* retains its physiological connection with the plant until the embryo has produced cotyledons and a root.

15. In the early autumn *S. apus* sheds all strobili whether fertilization has occurred or not. *S. rupestris* retains its stroblii throughout the winter and fertilization occurs in the spring.

16. *S. apus* forms twelve to fifteen megasporangia in each strobilus, all of whose spores are generally fertile. The comparatively limited number of embryos formed is due probably either to the limited number of fertile microspores, or to mechanical difficulties in the way of fertilization, possibly both. *S. rupestris* produces strobili far in excess of the number of purely vegetative branches, the majority of which develop only sterile spores except under very favorable conditions. The sterile spores are shed profusely during the summer, and the strobili which remain on the plant throughout the winter retain their power of apical growth. The first sporangia formed in the early spring contain microspores. There is but a limited number of these; then follows under favorable conditions either fertilization or the development of megasporangia, which continues until checked by the development of embryos in the older regions of the strobilus, or in case fertilization fails by the approach of winter.

TECHNIQUE.

The tender tips of the strobili offer no special difficulties in preparation for the microtome, but the older sporangia, especially the closely compacted strobili of *S. rupestris*, are exceedingly resistent to the entrance of reagents, and the hardened epidermis of the sporophyll, combined with the thick walls of sporangia and spores, render sectioning difficult. Certain stages of the spores are peculiarly liable to collapse. These technical difficulties probably explain many gaps in our knowledge. The following method was followed in preparing the material for this investigation.

KILLING AGENTS. — Flemming's weaker fluid, Hermann's chromacetic acid, and bichromate of potassium combined with acetic acid, gave the best results. Corrosive sublimate, absolute alcohol, picric acid, Merkel's and Perenyi's fluid were tried, but the results were unsatisfactory in that I failed to get such successful staining after their use.

These fixing fluids were used boiling hot. In the case of the Flemming, the chromic acid and water were brought to the boiling point, the osmic and acetic acids quickly added and the mixture poured over the strobili which had previously been removed from the plants. The vessel was covered tightly and the contents allowed to cool gradually to a temperature of 30° C. The spores were fixed in twenty four hours, but often were left in the killing fluid two or three days with no deleterious effects. Water of approximately the same temperature (30° C.) was used for washing, in very large quantities, and changed frequently for two days. Sometimes it was more convenient to use cold running water, in which case three days' washing was necessary to remove all acid. The dehydrating process was equally gradual: twelve hours each in 10 per cent., 20 per cent., 30 per cent., 50 per cent., 75 per cent., and 80 per cent. alcohol respectively. In 95 and 100 per cent. three days each, and the alcohol changed each day. Xylol was added to the specimens with even more caution, as an examination of material from day to day during these manipulations disclosed the fact that at this point danger of collapse was greatest. Six intermediate grades between absolute alcohol and pure xylol were employed, each for twenty-four hours. The strobili remained in pure xylol until they became transparent, which frequently was not for a week, dependent upon the age of the spores. When this condition was obtained, the xylol was replaced by fresh, and small bits of soft paraffin (melting point 30° C.) were added gradually as long as they would dissolve at the temperature of the room. This usually required two days. Thence the vessel was removed to the bath (temperature 40° C.), which was raised slowly to 54° C., soft paraffin being added

during the time up to the point of saturation. At this time the cover was removed from the vessel to facilitate the evaporation of the xylol, and harder paraffin added in small quantities at intervals. At the end of two or three days the temperature was raised to 65° C., and maintained for one week, after which time the xylol had evaporated, and the strobili were infiltrated with paraffin.

At first, on the supposition that such protracted exposure to reagents and heat would injure the more delicate very young sporangia, the tips of strobili were removed, carried through the various media in much less time, and subjected to a temperature of 50° C. for about ten hours only. Comparisons later showed that these precautions were unnecessary, and that the longer exposures produced better results, even in the apical cells. Moreover, having a strobilus cut *in toto* was of the greatest value in interpretation. Further experiments prove that considerable latitude in the direction of longer periods of immersion in the various fluids are not injurious, but all attempts to hasten results by shorter exposure than the period stated above were unfortunate. By an oversight, at one time the temperature rose in the bath three successive nights to 75° C., but with no injurious effects. Some difficulty was experienced in imbedding. The paraffin was inclined to shrink away from the rough surface of the spore wall, which caused the sections to drop out of the paraffin ribbon when transferred to the slide. The difficulty was overcome by removing the strobili to the imbedding dish from the bath, letting them cool off slightly (to about 40° C.), pouring on paraffin at a temperature of 80° C., then cooling as rapidly as possible in ice water. No further trouble was experienced and the strobili could be sectioned without difficulty.

STAINS.—The best stains for the youngest stages of sporangia are iron haematoxylin (Haidenhain method), and the so-called Flemming triple stain—saffranin, gentian-violet, and orange G. Frequently gentian-violet and orange G were employed without saffranin; for the gametophyte development,

after the appearance of the proteid matter in quantities that obscured the other cell features, cyanin and erythrosin, after treating the sections on the slide with dilute sulfuric acid and chloroform, produced very satisfactory results. The power to take up the stains was retarded in the case of the proteid granules, whereas the nuclei and cell walls were more readily and more brilliantly dyed after this treatment. Karyokinetic figures were especially clear.

It remains my pleasant duty to express my thanks to Dr. John M. Coulter, and to other members of the Botanical Department of the University of Chicago, for many suggestions offered in the course of this investigation. To Mr. E. J. Canning, Head Gardener of the Botanic Gardens of Smith College, I am deeply indebted for aid in collecting and growing material.

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EXPLANATION OF PLATES V–IX.

All figures were drawn with the aid of a camera lucida and a Bausch and Lomb microscope, and were reduced to one fourth their original size in reproduction.

PLATE V. Selaginella apus. Oc. ¾, oil immersion $\frac{1}{12}$.

FIG. 1. Vertical median section of tip of strobilus showing the apical cell, a young sporophyll whose apical cell is just established, an archesporial cell (shaded), and a two-celled sporophyll (distinguished by black nucleoli).

FIG. 2. Radial section of portion of strobilus showing sporophyll and two superposed cells (shaded), resulting from a transverse division of the archesporial cell. The superficial cell by repeated division in one plane

eventually forms the initial sporangium wall. The hypodermal cell is the initial sporogenous cell. The first cell of the ligule is distinguished by a black nucleolus.

FIGS. 3 and 4. Radial section of portion of strobilus showing two superficial archesporial cells (shaded).

FIG. 5. Radial section of strobilus showing three-celled sporophyll (near apex), a two-celled sporangium (shaded) near the base of the subtending sporophyll, and the early stage of the vascular system.

FIG. 6. Radial section of strobilus showing four-celled sporangium possibly formed by two archesporial cells which divided by transverse walls. A stage subsequent to *figs. 3* and *4*.

FIG. 7. Radial section of older sporangium. Sporogenous cells are shaded, and are represented with black nucleoli.

FIG. 8. Vertical section of sporangium showing definite radial arrangement of cells and plane of cleavage dividing it into two groups of cells, each the progeny of one of the two superficial archesporial cells shown in *figs. 3* and *4*.

FIG. 9. Vertical median section of sporangium more advanced. Sporangium wall at this stage consists of one layer.

FIG. 10. Median transverse section of sporangium showing the sporangium cells, the tapetum, the inner and the outer layers of the sporangium wall.

FIG. 11. Section of sporangium after the spore mother cells are established. In this stage the sporogenous cells are distinguished by two conspicuous masses of granular matter which lie against the nucleus.

FIG. 12. Group of sporogenous cells in synapsis stage. Probably microspore mother cells.

FIG. 13. Detail of small portion of megasporangium showing megaspore mother cell (distinguished by the lumps of matter on either side of the nucleus) lying near the glandular tapetal cells. Two sterile sporogenous cells are at the left and below the megaspore mother cell.

FIGS. 14–24. Stages in the development of the megaspores. *Fig. 16* shows the characteristic sextuple spindle stage previous to the separation into spores, as seen in *fig. 18*. The four nuclei pass from the bases to the apices of the newly formed spores, as shown in *figs. 18–22*.

FIGS. 25–28. Details of cell division in the final stages of development of the female prothallium. *Fig. 25* represents a portion of a section of the stage represented in *fig. 49* to show thickness of protoplasmic vesicle and the invasion of fibrillae blocking off the separate nuclei.

FIG. 29. Section of archegonium. The egg and ventral canal cell are lying in a plane perpendicular to the long axis of the archegonium. The egg is the larger cell with black nucleus.

FIG. 30 Section of archegonium in which the egg lies below the ventral canal cell, and the neck canal cell above it. Two tiers of neck cells are drawn.

FIG. 31. Stage younger than that shown above, before neck cells are cut off.

FIG. 32. Archegonium with egg and ventral canal cell laterally placed. No trace of neck canal cell. Neck consists of four tiers of cells, each tier comprising an upper (superficial) cover cell, and one neck cell. The cells abutting on the venter belong to the prothallium.

FIGS. 33 and 34. Mature archegonia. In *fig. 33* a spermatozoid is lying on the receptive spot of the egg. *Fig. 34* shows a one-celled embryo.

PLATE VI. Selaginella apus. Oc. 2, oil immersion $\frac{1}{12}$.

FIG. 35. Section of young megasporangium at earliest stage when megaspore mother cell is distinguishable from sterile cells. For detail see *fig. 13*.

FIG. 36. Section of older stage of megasporangium. Megaspore mother cell has moved near center of sporangium.

FIG. 37. Oblique section of megasporangium showing young tetrad, and sterile mother cells, floating in slime composed in part of disintegrated sterile cells and in part of a secretion poured out by tapetum.

FIG. 38. Section of somewhat older stage of megasporangium containing group of four megaspores (only three are represented). Each spore consists of an outer coat, the exospore; a median layer which is later differentiated into the mesospore and the endospore; a vesicle of protoplasm containing a limpid fluid and possessing a very small nucleus. The spaces intervening between vesicle and median layer and between the latter and the exospore are filled with fluid.

FIGS. 39–41. Successive serial sections of a tetrad, to illustrate the fact that the exospore is a continuous envelope common to the group of spores and splits as they move apart.

FIG. 42. Section of group of megaspores but little older than those in *fig. 38*. Filamentous processes shown between spores. The mother cell membrane, beyond whose boundary the radiations do not pass, envelops the tetrad.

FIG. 43. Section of two megaspores more advanced. The spore at the left is cut nearly in half from apex to base, that at the right is a slice across the apex. Protoplasmic vesicle grown but little larger than in *fig. 42*. Spine-like processes upon exospore in connection with radiations. Mother cell membrane still evident.

FIG. 44. Section of the female gametophyte showing the protoplasmic vesicle with two nuclei. The radiations extend across the spaces between vesicle and median layer, between median layer and exospore, and between the latter and the original spore mother cell membrane.

FIG. 45. Section of female gametophyte whose vesicle has five nuclei and no cell walls. The exospore has grown to the size of the megasporangium as shown in *fig. 38*. The median layer has divided into the endospore (represented in section as a broad black band), and the mesospore which can be distinguished only as a delicate layer (represented by a single line) just without the endospore. The exospore is of spongy appearance and is still in contact with the persistent spore mother cell membrane. Fluid, presumably protoplasmic in nature, fills intervening spaces.

FIG. 46. A transverse median section of a female gametophyte in "film" stage. The megaspore, endospore and protoplasmic vesicle (studded in its apical region with large free nuclei) have stretched to the dimensions of the exospore, against whose inner surface they form a layer consisting of three delicate lamellae. The central vacuole is filled with clear fluid. The same stage is shown in *figs. 47* and *48* the former representing a surface view, the latter a median section.

PLATE VII. Selaginella apus.

All figures except 56 and 58 drawn with oc. 2, obj. $\frac{1}{6}$. *Fig. 56* is drawn with same combination as plate V; *fig. 58* with oc. 2, obj. $\frac{2}{3}$.

FIG. 47. Surface view of the protoplasmic vesicle as if seen through spore walls.

FIG. 48. Vertical median section of the same stage. The nuclei are massed in the apical region and the interior of the vesicle is occupied by a vacuole.

FIG. 49. Surface view of the gametophyte at the moment when protoplasmic fibrillae appear in the apical region and radiate over the surface of the gametophyte. The nuclei in the lower part of the figure are in process of division. The vesicle has increased in thickness (cf. *fig. 50*), and is beset with proteid granules. Contents of vacuole a homogeneous liquid.

FIG. 50. Median section of same.

FIG. 51. Median vertical section of female gametophyte. Protoplasmic vesicle much thicker in apical region where the nuclei are disposed in several layers diminishing to a single one in the equatorial region. Fibrillae permeating the nucleated portion have outlined indefinite areas but there are no cell walls. Contents of vacuole an emulsion.

FIG. 52. Section showing a portion of the megasporangium with female gametophyte *in situ* to show the differentiation of the wall. In the lowermost part of the figure the fragile cells of the area of dehiscence are seen in cross section. The inner layer of the wall probably supplies the outer with nourishment. The vestiges of the tapetum are upon its inner face, as a pavement layer, and a few sterile mother cells lie at the left next the wall.

FIG. 53. Vertical median section of female gametophyte showing the differentiation of cells into an apical superficial layer from which develop

archegonia, and a lower vegetative region. The delimitation of the archegonial region is shown by the trefoil shaped cleft seen in the lowermost spore of *fig. 58*.

FIGS. 54 and 55. Section of female gametophyte showing archegonia. Details of the process of division in the unshaded cells of *fig. 54* are represented in *figs. 26–28*.

FIG. 56. Two embryos, one of two cells, the other of three, lying side by side in one venter. All walls shown are parallel to the axis of the archegonium. Compare relative position of these embryos with that of the egg and ventral canal cell in *figs. 29, 32*.

FIG. 57. Embryo *in situ*. The root lies toward the apex of the gametophyte. At the right the club-shaped foot of large cells is embedded in the prothallial tissue. The embryo is bent with respect to its long axis so that the stem apex and cotyledons are brought nearer the root than appears in the drawing, which is a reconstruction from serial sections. The two leaves with their relatively large ligules are developed successively and envelop the tip of the stem (shown by dotted line). The embryo is still within the spore wall and sporangium.

FIG. 58. Vertical section of megasporangium containing three female gametophytes. The lowermost shows the trefoil-shaped cleft in the apical region of the spore wall, exposing the archegonia. The two other oblique sections are not so advanced in development. The pad of tissue at the base of the sporangium lies above a region of storage cells in contact with the vascular bundles of axis and sporophyte.

PLATE VIII. Selaginella apus.

All drawings made with oc. $\frac{3}{4}$, oil immersion, obj. $\frac{1}{12}$, excepting 60–62. Figs. 60, 61 were drawn with oc. 2, oil immersion, obj. $\frac{1}{12}$. Fig. 62 with oc. $\frac{3}{4}$, obj. $\frac{2}{3}$.

FIG. 59. Section of microsporangium, showing microspore mother cells, tapetum, inner and outer layers of sporangium wall.

FIG. 60. Median vertical section of microsporangium with mother cells in synapsis stage. Sub-archesporial pad developing at base of sporangium.

FIG. 61. Slightly oblique section of microsporangium showing microspores in groups of four (tetrads).

FIG. 62. Median vertical section of microsporangium to show sporangium wall at maturity. Dehiscence region cut across at apex. Sporangium opens in two valves, the subarchesporial pad at top of pedicel serving as a fulcrum.

FIGS. 63, 64. Microspore mother cells during first division of nucleus.

FIGS. 65, 66. Sextuple spindle stage with nuclear plates.

FIG. 67. Exterior view of young microspore.

FIG. 68. Section of tetrad, showing continuity of exospore around the four microspores, and spore mother cell membrane enveloping the tetrad. The protoplasm is a thin vesicle with a single nucleus, parietally placed, and surrounding a large central vacuole.

FIG. 69. Exterior view of mature microspore showing pebbled exospore.

FIG. 70. Vertical section of male gametophyte after first division of spore into generative and vegetative cells.

FIG. 71. Male gametophyte as seen by focusing through spore coats. The large generative nucleus lies near the wall, the vegetative cell not in focus.

FIG. 72. Male gametophyte showing generative cell in section.

FIG. 74. Male gametophyte showing lenticular vegetative cell at left. The remainder of the content constitutes the generative cell with a centrally placed nucleus. Masses of deeply staining proteid matter appearing.

FIG. 75. Section of male gametophyte in which masses of proteid matter have increased in number. Vegetative cell appressed to wall at left.

FIG. 76. The protoplasm is aggregated around the centrally placed generative nucleus and has sent out radiating processes, connecting it with a peripheral layer. The vacuoles thus isolated are filled with a semi-fluid granular matter.

FIGS. 77, 78. A common appearance, where a large symmetrical mass of proteid matter (solid black) in the central vacuole may be mistaken for a nucleus.

FIG. 79. First division of generative nucleus. Persistent vegetative cell appressed to wall in lower portion of figure.

FIGS. 80–87. Phases of the early divisions leading to the spermatozoid mother cells.

FIGS. 88–95. Sections in various planes showing the two cell complexes and their relation to the dissolving proteid masses by which they are enveloped. The masses of food matter are separated by strands of protoplasm in *figs. 88, 93, 95.*

FIG. 96. Exterior view of male gametophyte displaying trefoil shaped cleft in apical portion. The complexes of spermatozoid mother cells protrude through the gap.

FIG. 97. Male gametophyte with spermatozoid mother cells as seen by focusing through spore coats. The unusually persistent vegetative cell is represented lying above the mother cells.

FIGS. 98, 99. Male gametophyte at maturity. The endospore protrudes like a short pollen tube through a gap on the ruptured exospore, and contains a slimy homogeneous fluid which later is discharged with the spermatozoids.

FIG. 100. A transverse section of a female gametophyte displaying the

eggs and spermatozoids. The necks of the archegonia have been sliced off somewhat obliquely.

PLATE IX. Selaginella rupestris.

FIG. 101. Apex of a strobilus in radial section. A single archesporial cell (shaded) at the base of a sporophyll. The cell with black nucleus is the initial cell of the next younger sporophyll of the same rank.

FIG. 102. First division of archesporial cell into a hypodermal and a superficial cell.

FIG. 103. The superficial cell of the first division has divided into three wall cells, and the hypodermal cell into two sporogenous cells, forming a wedge-shaped mass.

FIG. 104. Radial section of portion of strobilus. The largest sporophyll has ceased to grow at the apex which is converted into a branched spine. The initial cells of the ligule at the base of the sporophyll are represented with black nuclei. The tissue is rupturing to form air chambers in the basal region. The sporangium has been outstripped in growth by the sporophyll next above it. The two shaded cells in the upper part of the figure represent the same stage of sporangium as seen in *fig. 102*.

FIG. 105. Section of sporangium. The wall is nearly completed and the tapetum is becoming differentiated from the sporogenous complex of cells. The limits of the latter in the basal region not so clearly defined as repre sented in the figure.

FIG. 106. Detail showing two megaspores and several sterile mother cells.

FIGS. 107–117. Phases undergone by megaspore mother cells preceding divisions into spores.

FIG. 118. First division of megaspore mother cells into two spores.

FIG. 119. Section through sister megaspores. A portion of the sculptured exospore is removed from the upper surface of each, showing the proto-plasmic vesicle with a small nucleus floating in liquid. The spore mother cell membrane envelops the two spores.

FIG. 120. Section showing incomplete division of the protoplasm of two megaspores. The nucleus of the spore mother cell has not divided.

FIG. 121. Section through a single megaspore whose contour and large nucleus suggest that it is the direct product of a spore mother cell which has failed to divide.

FIGS. 122, 123. Older stages of megaspores.

FIG. 124. Median vertical section of tip of strobilus showing relation of sporangia to sporophylls and vascular system. The meristematic regions at the bases of the sporangium pedicels grow upward slightly by causing the megasporangia to appear sunken in the hollows thus formed. There were only megasporangia in this strobilus.

FIG. 125. Transverse section of strobilus through microsporangia. In the center of the figure is the axial strand surrounded by air chambers interspersed with meristematic tissue. At the right and left are two microsporangia, each showing the septum which incompletely separates it into two loculi. The rest of the diagram represents the cross sections of six sporophylls with their ligules.

FIG. 126. Apical portion of strobilus showing young sporophytes protruding from undetached megasporangia.

HULL BOTANICAL LABORATORY,
THE UNIVERSITY OF CHICAGO.

THE ECOLOGICAL RELATIONS OF THE VEGETATION OF WESTERN TEXAS.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. XXX.

WILLIAM L. BRAY.

(WITH TWENTY-FOUR TEXT FIGURES)

[*Continued from p. 123.*]

THE GREAT PLAINS.

THIS great region is naturally divided into two sub-regions, (1) the prairie plains, from which, except for scattered remnants, the original Great plains deposits have been removed, and embraced in the central and east central provinces of Hill (*fig.* 1); and (2) the remaining areas of Great plains proper (Llano Estacado, Edwards plateau, and Stockton plateau).

The prairie plains.—This sub-region embraces the grass country of central and north Texas west of meridian 97.5°, an area over 50,000 square miles in extent. As previously stated, it is a vast region of denudation, presumably from a former plain which must have stood at a much higher level. Whatever may have been the overlying formations, the present stage of erosion presents exposures of various formations, each of which owes its individuality chiefly to the character of the strata now undergoing reduction. Taken as a whole the dominant vegetation is a grass formation, but upon the areas of sand and gravel exposure, and the hills, bluffs, and streamways, timber formations prevail. The provinces are the Grand prairie and those of the central denuded region, embracing (1) the granite country, (2) the Carboniferous area (Brownwood and Palo Pinto countries), (3) the upper cross timbers, (4) the red beds country, and (5) the Callahan divide.

THE GRAND PRAIRIE—Geologically this is a Lower Cretaceous area extending from the Colorado river (its eastern

margin near Austin) northward beyond the Red river, its eastern boundary being the Black prairie or rich black land area of Texas. The western boundary of this province is a prominent and irregular escarpment overlooking the central denuded region, and the upper cross timbers at the north. The prairies, which are the dominant physiographic feature, are wide undulations interrupted by broad erosion valleys and occasional butte remnants of the former plain. The elevation of the province is from 800 to 1200 feet. The soil covering is but a thin veneering overlying alternating beds of chalky limestones and marls, which are very poor receivers or retainers of moisture. This condition suffices to offset the comparatively high annual rainfall (28 to 32 inches), so that this is a province of pronounced xerophytic grass formations, but still a transition from the mesophytic Austro-riparian to the xerophytic Lower Sonoran zone. In its temperature relations the province stands almost on the transition to the Upper Sonoran and Carolinian zones respectively, thus differing notably from the Rio Grande plain province which passes into semitropical.

Pure grass formations.—Ecologically the grass formations are strongly xerophytic and partake of the characters of the grass vegetation of the more westerly plains, though in a moderate degree. As already seen, the mean annual rainfall is sufficient, other things being equal, to give existence to semi-mesophytic formations. But the periods of brilliant sunshine and dry air which prevail, especially during the growing season, very quickly dry out the superficial covering of soil and drive vegetation into the resting stage. Under present conditions of pasturage the grass covering has been sadly reduced from its former occurrence. Formerly it was very compact and luxuriant. With the breaking up of this, moisture relations have changed, and the formation is now more xerophytic. Floristically it is impossible to say, with the meager data available, how the association of species compares with that of prairies and plateau plains westward, or to what extent the formation has changed under pasturage. It is certain from the general aspect of the formation, however,

that the dominant species here are not dominant ones on the more western plains. In brief, the ecological type known as prairie grasses exists here, as distinguished from the high plains type.

The grass vegetation of the Grand prairie is accompanied by a very abundant vegetation of prairie annuals and herbaceous

FIG. 7.—Rio Grande chaparral at Laredo: sage (Leucophyllum), "all thorn" (Koeberlinia), Mexican persimmon (*Diospyros Texanum*), and eight or ten other species.

perennials, with lignescent, tuberous, or bulbous underground parts. These assist in giving the province individuality as a grass formation.

Formations of prairie annuals.—Since the most conspicuous formations of this kind occur in other provinces, this type will be discussed later under a separate heading.

Chalk soil formation of herbaceous perennials.—The species associated in this formation number perhaps thirty-five or forty. It occurs throughout the province on the thinnest soils, but comes

out especially on bare chalk slopes. Sometimes a single species prevails upon such places, but commonly there occurs a mixture embracing nearly all the species. Thus a careful collection upon a typical chalk area will yield more than three fourths of the species of the typical formation (*fig. 14*).

In all species the underground parts are reservoirs of food (and not infrequently of water) protected against the extremes of heat and drouth to which the arid soil is subjected. When the soil is wet by rains these subterranean organs quickly throw up vegetative organs, and perhaps flower and mature fruit before the brief period ends and they are again driven into the resting stage. The underground parts are of several types, as succulent fibrous roots with a thick zone of mucilaginous or saponaceous tissue (*Krameria secundiflora*, *Yucca rupicola*); woody subterranean tuberous caudex (*Liatris pycnostachya*); mucilaginous bulbs with impervious coats (Allium, Cooperia), and deep irregular or fusiform roots with hard flinty (sclerenchymatous) coat (*Asclepias decumbens*).

THE CENTRAL DENUDED REGION.—The granite and Carboniferous areas and the upper cross timbers together constitute a belt lying below the western escarpment of the Grand prairie, where the prairies are more or less interrupted by a more broken relief, which in part of the granite area becomes positively mountainous. This belt is marked on the more level areas by a surface covering or by deep beds of sand and gravel, where conditions favor the occurrence of an open timber formation and even a close forest covering in the upper cross timbers. Discussed from the standpoint of grass formation, the granite and Carboniferous areas (Burnet, Brownwood, and Palo Pinto countries of Hill, see *fig. 1*) are open-timber grass prairies, which with the spread of the mesquite (*Prosopis juliflora*) are losing their last remnants of pure grass formation.

The grass formation of this belt (the upper cross timbers not included) appears to have about the same character as that of the sand plains of the Rio Grande plain. The ecological conditions are very similar except as to temperature, and the results

of this difference are apparent even superficially in the absence of certain semi-tropical species common at the south, and in the presence of Upper Sonoran or Carolinian species whose range extends into the middle northern states.

THE RED BEDS PROVINCE.—The vast level plains of reddish, chocolate soil make of this province one of the most unique features of the entire Texas region. This geological formation underlies the Staked plains, and has been exposed by the erosion of that area in the Pecos and Canadian river valleys. But the red beds plains lie between the Staked plains and the Grand prairie (more accurately the upper cross timbers), a width of 150 miles, and stretch away through Oklahoma and southern Kansas, a distance of 400 miles. Erosion and weathering have left wide, flat stretches of reddish landscape, either covered with fine, chocolate, silty sand, or exposing the bare rock. Violent bursts of rainfall wash away acres of prairie, often to the depth of several feet, carrying the chocolate flood silt to the coast country. Within the Texas region there are no large relief features in the red beds province, although the broad erosion valleys have to a certain extent the "Bad lands" aspect. The great extent of this province and its geographical position give it climatic relations which are apparent in the character of the vegetation.

As to atmospheric moisture, the stretch of 150 miles (the breadth of the province) from east to west means a variation in rainfall from 27 to 20 inches, and of evaporation capacity from 50 to 65 inches. The vegetation of the western part of the province has a more extreme xerophytic character than that of the eastern part. The northeastern parts sustain extensive mesophytic or semi-mesophytic culture formations with reasonable certainty. It is particularly a wheat belt. Toward the western border these formations become impossible except with seasons of higher rainfall.

As to temperature, while the entire province falls in the Lower Sonoran zone, its position as a whole far to the north of the Rio Grande plain gives it floristic relations more in common

with the Upper Sonoran areas to the north. But within the province itself there exists this diversity, that the southwestern border receives much from the arid Sonoran flora of the southwest, at the northeast the incoming flora is a semi-mesophytic one from the northern prairies. This relation to the flora north-

FIG. 8.—Edge of chaparral thicket, Port Lavaca.

ward is promoted by the continuation of the red beds formation as far as southern Kansas.

The ecological conditions are most favorable for a pure grass plains formation. While it lies beyond the zone of chaparral formations, the mesquite already covers most of the western half of the province, undoubtedly modifying the structure and content of the grass formation. As to the general type of grass formation, the semi-arid climate makes of this a characteristic dry grass plains flora. Without a more specific study of this flora it will be impossible to show satisfactorily wherein lies its

individuality as compared with the Grand prairie on the east and the Edwards plateau and the Staked plains on the south and west. It is probable that there is a real distinction, and that it lies chiefly in the peculiarities of the red beds formation. Two specific formations are constantly to be distinguished, (1) the *Hilaria Jamesii* formation, which occupies the lower stretches where sandy loam lies deeper, and appears like a vast field of heavy cultivated hay; and (2) the *Aristida fasciculata* formation, which occurs on ridges alternating with the lower areas of *Hilaria Jamesii*, and in its turn presents large tracts of waving grass fields.

Formations of prairie annuals.—It is not possible at present to say to what extent or wherein the prairie annual formations are distinct from those of other provinces. The soil conditions are such as to favor many species devoted to sandy soils. In the southern part of the province there are species from the south and southwest. At the north the prairie annual flora of Oklahoma and Kansas, in the same longitude, appears to be largely predominant. These formations prevail in such abundance in the case of some species as to form an important factor in the forage supply, especially in the early spring, when there is a solid mass formation. This disappears before the climax of the grass vegetation season (*fig. 17*).

The Great plains proper.—There are included in this region three provinces of the higher plains, namely Edwards plateau, the Staked plains, and the Stockton plateau (*fig. 1*).

THE EDWARDS PLATEAU.—This province forms the continuation of the Great plains east of the Pecos, from the southern limit of the Staked plains to the downfall at the Balcones escarpment overlooking the Rio Grande plain. The entire southern half between the Colorado and Devils rivers is marked by such deep erosion as to be mountainous. While a grazing country, this is not characteristically a grass plains, but a timbered area, and hence to be discussed especially under timber formations. But the grass vegetation even here contests for predominance, except on the most rugged hills.

The plains prairies.—To the northwest there is an area of the Edwards plateau which has not yet come to the stage of active and deep erosion, but is a typical open level plains country, with low relief lines of erosion remnants, and draws which lead into the cañons of the southern erosion area. This plains prairie is embraced approximately in the counties of Upton, Glasscock, Stirling, Concho, Crockett, Sutton, Schleicher, Tom Green, and Irion.

This Cretaceous area, both by its altitude and its westerly position, shares climatic conditions to a marked degree with the Stockton plateau and the Staked plains. As a result, the grass vegetation is of a more xerophytic character than in any of the provinces previously discussed. It is, in fact, almost fairly within the "short grass" country. Like the Grand prairie, this Cretaceous formation increases the xerophytic tendencies, so that here we find again a strong element in the perennial vegetation, which is more suffruticose than herbaceous, and made up of species with more xerophytic aspect and with affinities to the flora of the trans-Pecos provinces. But this element is in every way the counterpart of the chalk soil lignescent vegetation of the Grand prairie. In addition, the chaparral formations of the Stockton plateau and southwestward are encroaching upon this area.

The Staked plains.—The Staked plains of the Texas region are simply a continuation southward of the Great plains area of western Nebraska, Kansas, and eastern Colorado, but cut off from the main area by the deeply eroded channels of the Canadian river on the north, and the Pecos on the west. To the north of the cañon of the Canadian river, Texas contains also a portion (the Pan Handle) of the main body of the plains. "This province is a vast constructional plain made up of flood débris from the mountains at whose base it lies. This mass of loose unconformable stuff is a monotonously flat plateau plain, whose only surface relief is the billowy swells and the shallow saucer-like depressions" (Hill). The open, porous, often sandy texture of the soil furnishes a favorable receiving area for

rainfall. The soil water level is too far beneath the surface to be drawn upon even by deep-rooted trees. The vegetation is dependent, therefore, upon the immediate surface for its moisture, and alternates quickly between active growth and the dormant conditions according as the surface is moist or dry. But the porosity of the soil enables it to retain a larger percentage of precipitated moisture, so that the xerophytic conditions are not so extreme as the low rainfall (15 to 18 inches), the high

FIG. 9.—Characteristic occurrence of *Acacia amentacea* or black chaparral; on silty clay débris plain near Eagle Pass.

altitude (3500 to 4000 feet), the high evaporation capacity of the air (60 to 70 inches), and its high velocity would lead us to expect. The Staked plains do not terminate at the south in an escarpment, but pass into the plains portion of the Edwards plateau by a broken series of outlying buttes and sand hills and plains. These sand plains not only form the transition from the Staked plains, but extend northward nearer their western side beyond the center of this province.

In its temperature relations the Staked plains is mainly Upper Sonoran. The transition from Lower Sonoran is made about the 3500 foot contour. Beginning at the southern limit of the plains, the Lower Sonoran vegetation, notably the chaparral

formations, is represented in great strength. In going northward, ascending the plains, this vegetation becomes gradually more dilute, finally leaving a pure grass plain. The most apparent index of transition is furnished by the mesquite, which persists long after every other Lower Sonoran shrub has disappeared. Leaving a jungle of large mesquite below the escarpment, one comes upon a reduced growth upon the plains above, which becomes more and more dwarfed until at 3500 feet it is a mere clump of switches a foot tall, disappearing then absolutely. The same transition occurs in ascending the plains from the red beds province north of Red river, and where the Canadian cuts its cañon across the plains a Lower Sonoran flora has followed.

The grass formation of the summit plains is a solid grass floor of the short buffalo grass type. These grasses, in harmony with the sudden transition from moist to arid conditions, are adjusted to rapid changes from the dormant condition to luxuriant growth, and with the well-known characteristic that the growth already made when dry periods come on becomes perfectly cured as it stands, retaining all of the nutritious qualities which make these grasses economically valuable. All that remains alive during the dry periods are segments of the stem, which may be regarded as equivalent to buds or tubers or rhizomes. These are especially rich in carbohydrates. They are not underground nor connected with the soil by living parts, but merely anchored by the dead fibrous roots of the old growth. The cured grass serves naturally as a protective covering for the dormant living parts, although these are not often killed when the dry covering is burned off. Indeed, it is this quality of being able to endure fires that gives to these grasses the great advantage they possess in their constant struggle against woody vegetation (*fig. 23*).

The herbaceous species which accompany the grass vegetation are chiefly annuals. The lignescent rooted perennials so characteristic of the Cretaceous plains and prairies are mostly wanting, which is in harmony with the open porous soil texture. The very abundant *Yucca angustifolia* is an exception to this

fairly constant condition. As to their affinity floristically, these annual species, while containing a considerable element common to Texas prairies south and southwest, are those which range over the whole stretch of plains to Nebraska and the northwest, thus indicating more positively the Upper Sonoran character of the province (*fig. 18*).

The true value of the zonal areas of the Staked plains is not strongly brought out, because the dominant grass vegetation is not so sensitive to temperature differences. Yet it seems pretty certain, though not yet established, that some of the very important species of grasses found in southern and trans-Pecos Texas and north Mexico do not extend upon the Staked plains, but that rather the floristic content of the formation agrees with that of the plains northward.

The grass formation is broken on the sand plains of this province because of the shifting character of the sands. This sand zone according to Dr. Havard, is entered upon going about twenty miles west of Odessa. "It extends thence south and east nearly to the Pecos and north to the very center of the plains. In this zone are the sand hills, a dreary chaotic belt of reddish sand, tossed by the wind into hillocks, cones, and ridges of various sizes and shapes."[7]

The lower belt of the sand zone marks the transition from Staked plains to the Cretaceous Edwards plateau. This is the only portion of the sand plains of which we have data as to the plant formation. Dr. Havard says of it: "The only grasses seen were a stout Andropogon (near *A. furcatus*) three to five feet high, with running roots holding the loose soil in their meshes; a Sporobolus (probably a form of *S. cryptandrus*), likewise erect and tall; and a large form of *Cenchrus myosuroides*." This indicates that the characteristic plains formation is entirely wanting. The herbaceous annuals are also those which prefer sandy soils. It appears from Dr. Havard's report that woody vegetation is the more dominant formation.

THE STOCKTON PLATEAU.—This is a subdivision of the

[7] HAVARD, Contrib. U. S. Nat. Mus. **8**: (no. 29) 1885.

Edwards plateau, cut off by the cañon of the Pecos river. On the west the province adjoins the eastern front ranges of the mountains. Most of this area is a typical grass plain formation, of the general type found on the Staked plains and on the plains portion of the Edwards plateau. It will be seen that

FIG. 10.—Chaparral formation at Corpus Christi; the growth shown is not so tall as that which covers the country generally in this region; the genera are chiefly Opuntia, Condalia, Zizyphus, and Celtis.

nearer the Rio Grande the surface is more broken, and that here woody vegetation predominates, also that the chaparral formation is encroaching even upon the level grass plains.

Compared with the Edwards plateau, this province as a whole is more elevated, and is in a zone of less rainfall and of greater evaporation capacity. It is more intimately a part of the arid

plateau area of the Lower Sonoran zone, wich embraces north Mexico, southern New Mexico, and Arizona, and while it is only surmised that the grass formation would show this floristic relation, it is certain that other formations show it in a marked degree.

MOUNTAINS AND SOUTH PLATEAU SLOPE.

The Rocky mountains proper terminate before reaching the Texas region. The mountain axis continues southward, however, as an elevated plateau whose surface is much cut up by isolated mountain masses, some of which exceed 9000 feet in altitude. These masses are composed of Carboniferous limestone and sandstone, of Cretaceous limestone, and of igneous material. The high plateaus among them are mostly bolson basins filled with the débris of their bordering mountains. The soil conditions here and the moisture conditions growing out of these furnish the direct causes which operate to determine the distribution of plant formation in a region which possesses extreme xerophytic conditions independently of edaphic factors.

Viewed from the standpoint of the grass formation, this is a region possessing a grass floor climate in a surprising degree, for although the mountain masses are in some instances high and rugged, and covered with woody vegetation, the slopes of most of these up to 6000 and 7000 feet, the foothills, the wider plateau plains (for example, about Marfa and northwestward), and even portions of some of the desert bolsons, have a continuous grass formation. But in the mountains of the Great bend and their intervening bolsons (except in the Rosillos mountains, where good and available range grasses are found, according to Havard), on bolsons with loose wind-swept débris, and on arid gravelly mesas, there is only the most scattering bunch-grass formation, or even no permanent vegetation at all.

The bolson basins of this region, owing to the distribution of sedimentary filling, are lowest at the center and undrained. Consequently, the drainage water gathers at this place, in many cases accumulating in ponds or rather large lakes, and in all

cases making alkaline flats of varying degrees of saltiness. The higher, less alkaline slopes of these bolsons are often covered with grama grass formation characteristic of the region. The alkaline flats, of course, possess a halophytic vegetation, of which salt grasses form a prominent part.

On the whole, the grass vegetation of the mountain and south plateau provinces falls under three types of formation: (1) the close grass floor formation; (2) the open bunch grass formation; and (3) the salt grass formation. Of these the third will be discussed under the special head of "halophytic formations."

The open bunch grass formation is floristically equivalent to the close grass floor formation. The open and bunched character of the formation is due to extreme dryness, and especially to the instability of the loose finer igneous débris, or the coarser gravelly or stony nature of the soils.

The close grass floor formation may be designated "grama grass formation," from the popular name of the one to several prevailing species. In this formation, the great majority of species making up the formations of the eastern provinces have been sifted out by increasingly arid conditions, and only those remain which mark the extreme limit of xerophytic adaptation in grasses. A summary of the adaptation features of this type of formation shows: (1) rapid transitions from active to dormant conditions; (2) great resistance to extreme dryness and heat (including fires) while in the dormant stage; (3) equally great recuperative power after extreme treatment, including apparent extermination from a given area; (4) large food storage of fats and sugars in portions which retain vitality during dormant periods, thus rendering quick growth possible; (5) the quality of perfect drying *in situ*, thus not only covering the soil and holding it in place, but also protecting the vital parts.

PURE FORMATIONS OF PRAIRIE ANNUALS IN THE PRAIRIE PLAINS.

In the preceding discussion of grass formations, the herbaceous annuals of the prairies have been treated simply as accessory elements in the formations, but of value in characterizing

the formations differing somewhat in temperature and moisture conditions. But the annuals of the prairies in the west Texas region, as well as those in other parts of the Lower Sonoran zone, constitute a vegetation phenomenon which periodically overshadows everything else. This phenomenon is the annual wave

FIG. 11.— Hills covered with xerophytic timber, central mountainous region of Edwards plateau.

of vegetative growth and floral display which sweeps over the prairies, temporarily submerging the grass vegetation itself. In the mutual adjustment of grasses and herbaceous annuals in this climate, the latter, mostly pure mesophytes, must take advantage not only of the returning rainy season but of the optimum period preceding the intense summer heat, and of the absence of competing grasses at that time of the year. It is a matter of record among cattle men that in the early spring, when grass forage is scarce, their herds often feed largely upon the

abundant young vegetation of these prairie annuals. Thus the "tallow weeds" (*Actinella linearifolia* and *Amblyolepis setigera*), which cover many miles of range, are much prized. Not only does this annual vegetation sweep as a wave over the prairie in the early spring, but the individual species mass themselves in pure formations of incredible compactness and extent (*fig. 19*). Thus there may be successive waves of species. In harmony with the adaptation which leads to the massing of the species is the fact of the brilliance of floral display. This results in vast sheets of color. During the spring of 1900, which was unusually favorable for vegetation, the virgin prairie plains of Texas were literally a sea of color. In his survey of the Rio Grande plain during May, Vernon Bailey noted over twenty species which, as he expressed it, either occupied exclusively "acres of prairie" or "made miles of solid color." This was the case in the lower Rio Grande country (Corpus Christi to Brownsville) previous to May 10. The season of display ended about four weeks later on the northern boundary. At Austin by the first of July (often even two weeks earlier) a solid grass formation occupies the ground which had just previously been exclusively occupied by the "blue bonnet" (*Lupinus subcarnosus*). The continuity of grass formation seems in no wise disturbed by the periodical dominance of the annuals.

The species of these formations are of course dependent upon seed for their recurrence, and consequently are subject wholly to the caprice of rainfall during March and early April. When, as frequently happens, there is no rainfall of consequence during this period, the display of prairie annuals is very much reduced. Their adaptations are in the direction of seasonal adjustment rather than toward meeting xerophytic conditions.

II. WOODY VEGETATION.

Since the region under discussion includes only so much of Texas as is marked by a distinctly xerophytic vegetation, it follows that, except for river bottom and sheltered cañon timber, the woody vegetation is as a whole one of xerophytic aspect.

But it is of varying degrees of xerophytism according to its relation to the zones of decreasing moisture from east to west, that in the eastern provinces possessing some of the elements of the vast mesophytic forest of east Texas, while the extreme of xerophytism is reached in the desert bolsons of extreme west Texas. Recalling the common conception of the west Texas region as a grass country, it becomes a matter of surprise to learn how great is the proportion covered by woody formations, that is arborescent or shrubby vegetation in sufficient amount to form the chief covering.

This includes the following areas: the erosion area of the Edwards plateau; the hills, bluffs, and escarpment of the Grand prairie; the granite, Carboniferous, and upper cross timber areas; the higher mountain slopes and summits of the trans-Pecos mountains; the escarpment of the Staked plains and the Callahan divide; the chaparral of the Rio Grande plain, of trans-Pecos Texas, and of the lower Staked plains and adjacent Edwards plateau; the open streamways and the cañons; and finally many thousands of miles of mesquite-covered prairie. The energy and rate of encroachment of woody vegetation during the past half century lead one to believe that there is scarcely an area of consequence in the state that woody vegetation of some type will not occupy and cover more or less completely, granting of course that no artificial means are employed to check it.

The woody vegetation is here discussed under several types of formation, based largely upon moisture relations.

ARBORESCENT VEGETATION.

XEROPHYTIC FOREST FORMATIONS OF THE EROSION MOUNTAINOUS AREA OF THE EDWARDS PLATEAU (including the hill, bluff, and escarpment timber of the Grand prairie).—That portion of the Edwards plateau embraced between the Colorado and Devils rivers, and extending back 100 to 125 miles from the Balcones escarpment (southern downthrow of the Great plains) is very deeply cut by erosion channels, until the appearance is that of

a mountainous country. Here are found in full operation those agencies which have worn so much of the surface elsewhere from a higher to an approximately level lower plane. The Cretaceous limestones, which on the grass plains portion of the Edwards plateau lie still unbroken, have here been cut through

FIG. 12.—*Juniperus sabinioides* formation; a prominent feature in the xerophytic timber region of the Edwards plateau province.

and exposed on all sides, thus not only offering lines of penetration for tree roots, but moisture facilities not available from an unbroken level surface. By this erosion, also have come about unequal conditions as between the summits and slopes of the hills, and the gorges and cañons between them. Certain Cretaceous formations, friable on exposure to weathering, outcrop on the hill slopes or summits, thus exposing an unstable foundation for vegetation. On these outcrops, often entirely bare, certain very hardy species can secure a foothold, and so anchor

this crumbling rock, even permitting a soil accumulation. The existence of similar conditions in the exposed formations in the Grand prairie results in carrying the timber vegetation over the hills and bluffs and bordering escarpments of this province far to the northward of the main body (*fig. 11*). This timber formation is an open stunted forest covering, which suffers extensive interruptions, but continues in spite of this to be the dominant vegetation feature of the areas just described. On some high arid divides it becomes reduced almost to shrubby dimensions.

Floristically, the chief elements of this vegetation are Lower Sonoran, of which many species range southwest into the Mexican mountains, or westward across the continent. In the western part of this province the presence of western mountain species is very marked. At the east there remains a strong element common to the Austro-riparian and Carolinian zones; but, aside from these indications of relationship, the province has a strong individuality. This is well shown by the fact that Austro-riparian and Carolinian species (when not present in the cañon timber) are vicariously represented by species stamped with the climatic characteristics of the region. Perhaps the most noteworthy case is that in which *Juniperus Virginiana* is succeeded by *Juniperus sabinoides*, the latter being a most characteristic xerophyte.

As to the content of the forest formation, this may vary from a pure formation of one species to a more or less uniform mixture of 50 or 60 per cent. of all the species. This variation is generally due to variations in soil condition. For example, a pure formation of *Juniperus sabinoides* may be due to an extensive exposure of very friable limestone like the Glenrose beds. In some cases the prevalence of a single species is due to the accident of its having gained the ground first. The following species formations are the most notable in this province:

Juniperus sabinoides formation.—This is the most important formation, partly because of its ecological relations, partly from its economic value. The formation is popularly called "cedar brake." Such brakes may be almost impenetrable over many square miles. The tree branches diffusely from the ground up,

making a compact oval outline when standing free, and a dense interlacing of branches in close formation. Frequently at the ground the trunk itself divides into several approximately equal members. A pure formation of this juniper occurs characteristically where a friable limestone exposure lies almost bare of soil except a loose débris collected by the forest itself. Where such an outcrop occupies a slope whose angle is sufficient to make the friable rock surface unstable, an open cedar formation is the only woody vegetation present (*fig. 12*).

Aside from the very general use made of cedar in commercial ways, it occupies an important relation to moisture and soil conditions. Not only is the formation found to occupy areas where soil cannot accumulate except for the presence of this growth, but when cut or burned off it tends to reoccupy the ground most vigorously and to encroach upon the other species.

Quercus breviloba formation.—This is the so-called "mountain shin oak" of central Texas. On the summits of the high divides, where a thin soil is underlaid by unbroken limestone, the timber vegetation becomes very much dwarfed. In such cases the shin oak often becomes the dominant species and sometimes the only one, forming scrub thickets known as "shinneries." The mature plant may not exceed three or four feet in height. A familiar illustration of shin oak country occurs on the high divide between the San Gabriel and the Colorado rivers in Burnet county.

Quercus Virginiana formation.—This is in reality a dwarfed live oak formation which covers lower hill slopes or flats where the thin surface covering of black soil is strewn with coarse fragments of the broken underlying limestone. Such country, from its stony character is known as "hard scrabble," and the timber covering, often almost wholly of dwarfed live oak, is dwarfed and gnarled into a fitting counterpart of the ground structure (*fig. 13*).

ENCROACHMENT OF THE CRETACEOUS TIMBER FORMATION.—The forest covering of the erosion area tends not only to renew

itself when removed, but it is a vigorous agressor upon previously open untimbered areas. This persistence may well be turned to account in any plans looking toward the maintenance of the forest covering on the more arid hills for prevention of soil erosion and destructive floods.

FIG. 13.—*Quercus Virginiana* (mountain form) formation; Cretaceous hills fifteen miles west of Austin.

XEROPHYTIC FOREST FORMATION OF THE MOUNTAIN SLOPES OF TRANS-PECOS TEXAS.—This formation is the counterpart of that just described for the erosion area of the Edwards plateau. It is a part of the forest covering of the arid mountain slopes of the southwest, including south Colorado, New Mexico, Arizona, and northern Mexico. Its area in Texas is practically limited to the upper slopes of the mountains in the great bend of the Rio Grande (above 6000 feet); to the dry upper cañons in these mountains; to the middle slopes of the Guadalupe and Davis mountains and their dry cañons.

The ecological conditions of these mountain slopes are more

extreme than in the erosion area of central Texas, as shown in the following data. The annual rainfall is from 14 to 26 inches (approximate averages for each area respectively); the evaporation capacity is from 80 to 60 inches; the extremes of daily temperature in the trans-Pecos mountains is much greater than in the central region. Consequently the arborescent vegetation is one of more absolute adjustment to xerophytic conditions, and the semi-mesophytic species found in the central erosion area are either wholly excluded from the trans-Pecos area or relegated to the watered cañons. Of the arborescent species, *Pinus edulis*, *Juniperus pachyphloea*, *J. occidentalis*, *J. monosperma*, *Quercus grisea*, and *Q. Emoryi* are the principal ones. Not all of these are confined to the mountain slopes, for in watered cañons some of them form heavy timber of large size and good quality; but on the slopes their growth is dwarfed, the wood hard, the stems gnarled and misshapen, and they stand in a scant open formation.

The timber formation just described extends to certain physiographic features east of the Pecos river. These are the Staked plains escarpment, the remnant buttes of the Callahan divide (at least west of the 100th meridian), the sand hills of the southern Staked plains, and the cañon bluffs of the Devils and Nueces rivers. In the last instance, it is very dilute, being lost in the local formation, but in the other cases it is practically the only timber.

On the escarpment of the Staked plains, even as far as the northeastern border, there occur *Pinus edulis*, *Juniperus occidentalis* (in many straggling groves of small growth, according to Havard), and *Quercus grisea*. On the remnant buttes of the western half of central Texas there are close formations of a much dwarfed *Q. grisea*, in which this species attains a growth of only two to five feet, covering the ground in true chaparral fashion. Here also is found a very scattered formation of *Juniperus occidentalis*, which occupies also the lower mesas, becoming one of the chaparral species covering them.

On the sand hills of the lower Staked plains region one of the western mountain oaks (*Q. undulata* or *Q. Gambelii*) occurs in low thickets. To this region and the buttes and mesas eastward the trans-Pecos chaparral formation extends, and such reduced growths of *Quercus* and *Juniperus* as occur here become identified with the chaparral.

[*To be concluded.*]

UNIVERSITY OF TEXAS.

BRIEFER ARTICLES.

NOTES OF TRAVEL. VII.

A TROPICAL FOREST IN CERAM.

THE steamer Japara of the Netherlands India Packet Boat Company had a cargo of American pipe for a new oil well which was being sunk at Boela on the northeast coast of Ceram. To unload this pipe, the steamer anchored about noon on January 18 in the open roadstead, a half mile off shore. With our glasses Mr. Lathrop and I studied for some time one of those fascinating pictures of green and brown foliage which are the charm of steamboat travel in this tropical archipelago. We made up our minds that the low flat country and the hills behind it were covered with as rich a tropical forest as we had ever seen, but neither of us was prepared to find so many novel sights and interesting things as our short stay on land revealed.

Boela is a tiny clearing on the ocean edge of the forest, and not only has no harbor but its roadstead shoals so gradually that at low tide even a ship's boat grounds an eighth of a mile from the beach. So our party, the owners of the oil concession, the two travelers, and several native men and women, were forced to wade that distance before they reached the shore. The water was warm and our slight discomfort was quickly forgotten in the beauty or the oddity of countless things that attracted our attention.

As a first surprise, the beach was covered with thousands of moving shells of all sizes and shapes. These shells moved about in the most bewildering fashion. The rotting logs and even the mangrove bushes on the shore were literally alive with them. On examination each one was found to be the home of a hermit crab. Shells even smaller than the head of a shirt-stud were inhabited, and it was with difficulty that we found any uninhabited specimens. In our stay ashore we did not see a single hermit crab which had left its shell.

To add to this bewildering impression of moving strand shells, scores of small ash-colored fish were jumping about in the liveliest manner on the sand, often many yards from the water. These fish were

so quick in their movements that it was many minutes before our boy succeeded in capturing one with his hands. Although I did not observe any of these animals actually perched in the branches of the mangrove, I do not doubt the statement that they often climb low bushes near the strand, using their short ventral fins for feet.

Boela, the possible future oil city of the Orient, was decidedly in embryo. A few huts, made of the midribs of the sago palm and thatched with the matted leaflets of the same plant, were clustered about the landing shed and surrounded by young plantings of manihot, bananas, and a few papaya trees. At the end of the little village was a more or less comfortable bungalow in which lived an American mechanic from Pittsburg who had charge of the oil drilling machinery. Three of the most curious dogs I have ever seen greeted us as we walked up the path to the bungalow. They were crosses between the hairless Mexican dog and the "kampong" or native cur. These dogs were quite hairless except the tip of the tail, which was furnished with a brush of bright reddish-yellow hair, and the top of the head, which bristled with a stiff mop of the same color. The only cat of the place was one of the short-tailed breed which is common in this region.

As we strolled into the forest along a newly-made corduroy road, gorgeous butterflies flitted quickly or soared lazily across our path in such numbers that we were reminded of some of Alfred Russell Wallace's descriptions of his best collecting experiences in Malacca. Only twice before had we seen such quantities of these tropical insects, once on a small island in the gulf of Siam, and the last time on one of the pathways near Petropolis, Brazil. The newly fallen trees were swarming with insects and covered with fungi, and the log road was bright with red and yellow mushrooms of many different species. Every time we halted to examine a rotten stump or scratch away a few fallen leaves, swarms of black mosquitoes attacked us, and worried us with the suspicion that they were injecting malarial plasmodia into our blood.

The new oil well, which was soon reached, was surrounded by little pools of the dark brown liquid, and many tall forest trees about were killed by the crude oil which had flowed from the well before it was closed. The bubbling oil and gas was sputtering and hissing under the cap which had been screwed down to keep it in. Although inhabitants of Amboina who were interested in these wells expressed great hope of their success, as yet no large quantities of oil had been

discovered. The roads which were being cut into the interior were expected to open up and determine the size of this new oil field. Near one of the oil wells stood giant forest trees, with bases buttressed by thin irregular plates which reached to a height of ten or twelve feet from the ground. On one of these trees, twisting about its gray trunk, was an epiphytic fern with dimorphic leaves, the basal ones like saucers closely appressed to the thick fleshy rootstock which they protected from the bright sunlight and its drying action.

On the same tree, while examining this fern, we disturbed a number of large gray ants which had built a paper-like nest on one of the broad flat buttresses. Like a company of veterans they rushed out of the nest and ranged themselves at regular distances from each other about their home. Every ant stood upright, curled its abdomen upward between its hind legs as if ready to sting, and with waving antennae awaited the enemy. On the parchment-like walls of the nest these warriors, as they hurried out, beat a sharp tattoo which was much louder but similar to that sounded by the termite warriors on the thin wooden walls of their galleries.

The newly made roadways through the forest were strewn with fruits which had fallen from the tops of the tall trees. Some of these were of the brightest orange and others a clear lemon-yellow, others still were purple and brilliant green. None, however, were edible, though many were most attractive looking.

In the tree-tops overhead, bright green parrots chattered, and a small cicada with a shrill but not unpleasant note kept up an incessant racket. Once a black parrot with red head flew low through the trees, looking like a flash of crimson light. Most of the birds, however, were in this season in the tops of the highest trees.

As in all tropical forests I have ever visited, the flowers in Boela were scarce. One bright crimson representative of the lily family, with a spike as large as a pineapple, was the only showy species observed. The botanical fancy is attracted in these forests by the curious creepers, which fling their supple stems about the tall forest trees and spread out their dark green tops above those of their supporting neighbors, until the latter are robbed of sunlight and slowly die. There are curious masses of stilt-like roots from which rise tall slender trunks; the pendant barbed tips of the rattan palm catch and hold you; delicate masses of green filmy ferns form soft pads on the fallen trunks; dusky chocolate-brown masses of the myxomycete (Stemonitis)

color your fingers as you touch them; ugly looking incipient Polyporei exude oily looking drops of brown fluid; and the rotting bark contains a host of microscopic fungi. Epiphyllous algae and lichens are always abundant in these dark forests and are often mimicked by insects.

However little one may be interested in the insects of temperate regions, the constant buzzing of flies and wasps, and the fluttering of gorgeous butterflies in this virgin forest soon attract one, and leave a lasting impression of the activity of the animal world as compared with the world of plants. The ants alone, in their host of forms and curious habits, are sufficient to distract the most obstinate collector, and rob him of many hours he would have spent in adding new numbers to his herbarium. They are the most intelligent beings of the forest, and the solitary traveler finds a sort of intellectual companionship in watching their movements. The termites of the tropics are second only to the tree ants in interest. At Boela only the tree-inhabiting forms were found, and none of those curious kinds were seen which cultivate fungi in their nests. The dead stumps and trees were everywhere alive with them, and the decaying trees were rapidly removed by immense colonies of these wood-eaters. The virgin forests of the tropics would be well nigh impassible to collectors if the fallen branches and logs were not quickly riddled with the galleries of the white ants. They are above ground what the earthworm is below it. They reduce all dead wood to half-digested fragments.

This portion of Ceram is very sparsely settled, so sparsely, in fact, that during the whole time we spent at Boela we saw only two or three native Alfurians, who came off to the steamer in their small dug-out canoes to sell their large but coarse-grained bananas. They are a darker, more uncleanly race than the Javanese or Amboinese, and show traces of Papuan origin. Imported coolies from Java and Amboina are depended upon to work the drills at the oil wells.

But all idea of time was lost as we wandered through this forest, until the rapidly fading light (to say nothing of the rapidly devouring mosquitoes) gave warning that a hurried retreat must be made from this malaria-haunted shore. In the morning we saw Boela again, and it looked even more beautiful gilded by the rising sun than in the evening light. — DAVID G. FAIRCHILD, *Department of Agriculture, Washington, D. C.*

CURRENT LITERATURE.

BOOK REVIEWS.

The sea beach.

WE FANCY that there is a demand for a popular account of the seaweeds. It is not so important that the names and classification should be given, for such may be found in several well-written manuals and texts. What is probably most desired is a simple account of the life habits, and in part the life histories of such forms as are prominent in the tide pools, on rocky shores, in marshes, and in flats, and those that are washed up from the deeper waters after storms. A book by Augusta Foote Arnold[1] attempts to satisfy the thirst for seaside lore, and this review will discuss some points in her treatment of the marine algae. They are given only 50 pages in a book some 500 pages long, the remainder of the work dealing with the marine invertebrates, so it would be unjust to judge *The sea-beach at ebb tide* as a whole by the criticisms presented here.

It is hard to understand precisely the attitude of this author as regards the relation of popular science to technical science, or to put matters somewhat differently, the balance between the charm of natural history and the detail of a fully developed science. There is a little of both in this book, the science badly mutilated and sometimes incorrect, the natural history quite lacking the delicate fanciful touches that demand an imagination and yet must be tempered by many years of intimate contact with nature and by knowledge of scientific exactness and respect for it.

There is a brief account of the life habits, distribution, and uses of algae, and some statements about naming and classification which would lead the reader to suppose that especial emphasis would be laid upon these departments. And this is the case, for most of the space is devoted to the description and illustration of genera and species. These are apparently arranged after the system of a standard text, much abridged of course, the outline being presented at the beginning of each group. These synopses can be nothing but a mere dictionary-like table of names, for the account does not pretend to give the morphological characters of the groups. There are no keys, no microscopical examination is required, and for identification the reader (presumably beginner) must depend chiefly upon the figures. What

[1] ARNOLD, AUGUSTA FOOTE: The sea-beach at ebb-tide. A guide to the study of the seaweeds and the lower animal life found between tide-marks. Small 8vo. pp. xii+490. *figs.* 600+. New York: The Century Co., 1901.

then can be the value of this classification, out of sympathy with the purposes of morphology on the one hand and the spirit of natural history on the other?

The illustrations are photographs of mounted algae on cards, and in some cases of preparations slightly magnified. While many are clear others seem to the writer quite valueless as a means of identification and unworthy of the book. Although the color of the specimen would help in this mechanical matching of mounts with figures, nevertheless there is sure to be much confusion. For example, how is *Enteromorpha clathrata* to be distinguished from certain Cladophoras? The figure of *Ectocarpus viridis* might do for several other species, the Callithamnia are quite impossible, and *Polysiphonia fastigiata* is certain to be confused with Sphacelaria.

One occasionally finds statements that lead to the belief that the author is quite untrained in natural history. Thus, on page 29 is the phrase "*Ectocarpus Hooperi*, a species of Ectocarpus first described by Mr. Hooper." This does not seem to be a fact, and the impression conveyed that naturalists name species after themselves is an implication of conceit far from being warranted by the conduct of these modest members of society.

The book has yet to be written that will tell the natural history of seaweeds with the charm of manner shown in the style of Miss Margaret Morley. And until such a treatment appears, it is much better that the amateur collector and observer of marine algae read Murray's *Introduction to the study of sea-weeds*, a simple and very interesting account, and one thoroughly grounded in science.—B. M. Davis.

NOTES FOR STUDENTS.

Professor Arnoldi[2] has taken up the somewhat incomplete work of Shaw, and has made a careful study of the development of the endosperm of *Sequoia sempervirens*. Free nuclear division takes place in the usual manner in an evenly distributed peripheral layer of protoplasm, but very soon there is a denser accumulation of protoplasm at the lower end of the sac. When the formation of walls begins, three regions of the endosperm may be distinguished, the upper, the lower, and the middle. The upper, and particularly the lower, develop faster than the middle, so that the ends of the sac become filled with a solid tissue while the nuclei are still almost free in the middle portion. Each nucleus of the middle portion now becomes surrounded by a wall which is open on the inner side: the walls grow inward and when the center is reached, walls are formed at the inner ends of the cells. The nucleus now begins to divide, and each of these cells ("alveoli") becomes divided into several cells. Archegonia are formed only from these

[2] Arnoldi, W.: Beiträge zur Morphologie einiger Gymnospermen. I. Die Entwickelung des Endosperms bei *Sequoia sempervirens*. Bull. des Natur. de Moscow. Pp. 1–13. *Pls.* 7–8. 1899.

alveolar cells of the middle region. At the time of fertilization, the upper and lower portions of the endosperm consist of small-celled tissue, while the middle portion is alveolar. Sequoia is regarded as a connecting link between Gnetum and the angiosperms on the one hand and between gymnosperms and the archegoniates on the other.

In a later paper [3] he has described the archegonia and pollen tubes of the same species. The archegonia are very large, and some sections show as many as sixty. They sometimes occur singly, but are often grouped. In development they resemble the archegonia of the Cupressineae, since they are often in direct contact with each other and do not form any ventral canal cell. There are no proteid vacuoles. The neck consists of two cells, in this respect resembling the older gymnosperms.

The pollen tube grows through the nucellus, not between the nucellus and integument, as described by Shaw. At the time of fertilization the pollen tube contains the two male cells of equal size, and two small nuclei, one of which is the tube nucleus and the other "the nucleus of the cell which united the generative cell with the microspore wall." The general structure of the pollen tube and its contents agrees with the Cupressineae. The morphological considerations, together with the geographical distribution, lead to the conclusion that Sequoia is nearly related to the ancient type from which the modern Araucarias and Cupressineae have descended.—CHARLES J. CHAMBERLAIN.

CONNECTING THREADS which establish protoplasmic continuity between adjacent cells have been studied by Mr. Hill [4] in the embryo and seedlings of *Pinus pinea* and in the mature tissues of *P. silvestris*. Some attention was also paid to the endosperm of *P. pinea*. The endosperm consists chiefly of rather large rounded cells, but a close examination shows that in many cases an internal division has occurred. The threads are evenly distributed in the young walls, but are grouped in the older walls. Near the cotyledons the cells are smaller, the threads thicker, and there are traces of ferment action. Ferments from the cotyledon pass into the endosperm through the threads, and by the same route food materials pass from the endosperm to the embryo.

In the seedling the absorptive side of the cotyledon is more abundantly supplied with threads than the side not exposed to the endosperm. There

[3] ARNOLDI, W.: Beiträge zur Morphologie und Entwickelungsgeschichte einiger Gymnospermen. II. Ueber die Corpuscula und Pollenschläuche bei *Sequoia sempervirens*. Bull. des Natur. de Moscow. Pp. 1–8. *Pls. 10–11*. 1899.

[4] HILL, A. W.: The distribution and character of connecting threads in the tissues of *Pinus silvestris* and other allied species. Phil. Trans. Roy. Soc. London B. **194**: 83–125. *pls. 31–35*. 1901.

are no threads in the external walls of the epidermis, and but very few connecting the guard cells with their neighbors.

All parenchyma cells show a general resemblance in the character of their threads, the threads on the end walls being irregularly scattered, while on the side walls they are grouped. In the phloem all the sieve tube threads show a characteristic median dot. The albuminous cells at the edge of the phloem of the leaf have their threads grouped in localized thickenings on the walls, and serve to pass materials from the mesophyll to the phloem. The very numerous threads of the root cap form a connection with the free surface of the root and with the periblem.

In the mature tissue of *P. silvestris* the threads in the cortical tissue are similar to those of the seedling. In the phloem there is no connection between the sieve tubes and the bast parenchyma or the starch medullary ray cells. The sieve tube threads on the radial walls have a median dot. The torus of the bordered pit is probably traversed by threads which soon disappear. In the leaf, the distribution is about the same as in the cotyledon. The endodermis, with very numerous threads, is in close connection with the cortex and the stele. In the pericycle, living cells are connected by threads, but there is no connection between the pericycle and the lignified transfusion tissue.

In general, the main direction of threads in the cortex and phloem is tangential. The transitory nature of certain threads explains the absence of threads between the sieve tubes and medullary ray cells. Except in the medullary rays and in the cork cambium, the threads are chiefly on the radial walls. This suggests that in conifers food supplies and stimuli are conducted mostly in a tangential and vertical direction.—CHARLES J. CHAMBERLAIN.

OPEN LETTERS.

A CORRECTION.

In the June number of the BOTANICAL GAZETTE (31:441) there was published by Ernst A. Bessey, of the U. S. Department of Agriculture, a review of *Bulletin* 49 of the Oklahoma Agricultural Experiment Station entitled *A rhizomorphic root-rot of fruit trees.* The reviewer made the statement that "This has been shown by von Schrenk and others to be caused, in all probability, by a hitherto unidentified rhizomorph-producing fungus." The reviewer having failed, on request, to cite references to these publications of "von Schrenk and others" in support of his statements, and having thought it "inadvisable" to correct the same when asked to do so, the following brief statements are submitted for the information of those interested.

November 6, 1889, von Schrenk identified the fungus in question as "one of the most dangerous tree fungi known, *Agaricus melleus.*" (Letter to Horticulturist of the Okl. Agr. Exp. Sta.) Some more of the same material was submitted to Dr. B. T. Galloway, and under date of November 10, 1899, Dr. Galloway stated that "the fungus is the edible mushroom, *Armillaria mellea.*" (Letter to Horticulturist Okla. Agr. Exp. Sta.) In the *Orange Judd Farmer* for January 12, 1901, von Schrenk says, "I suspect that possibly the fungus when determined will prove to be the same as a fungus very common in both Europe and America, the *Agaricus melleus,* or honey mushroom." This last statement is quoted in the *Bulletin* of this Station above referred to.

These statements will show clearly the state of the investigations of "von Schrenk and others" at the time stated. Perhaps in the future we shall have from these sources some valuable publications regarding this subject, but at present none such exists to my knowledge. It is hoped the above explanations will clear away some misconceptions and prevent the inference that this disease had already been investigated by members of the staff of the Department of Agriculture.

E. MEAD WILCOX.

OKLAHOMA AGR. EXP. STA.,
Stillwater.

NEWS.

AT THE recent Denver meeting of the A. A. A. S. Dr. D. T. MacDougal was elected general secretary for the ensuing year.

THE University of Glasgow, at its ninth jubilee, celebrated in June last, conferred the degree LL.D. upon Professor W. G. Farlow, of Harvard University.

PROFESSOR F. O. BOWER of the University of Glasgow is one of three representatives appointed to attend the bicentennial celebrations of Yale University next October.

THE University of Chicago at its last Convocation conferred upon Mr. A. A. Lawson and Miss Florence May Lyon the degree Ph.D. Miss Lyon has been appointed associate in botany and Head of Beecher Hall in the University of Chicago.

M. EUGENE AUTRAN has severed his connection with the Boissier herbarium at Geneva, Switzerland, and has been appointed botanist to the botanical garden of Buenos Ayres. He is also a member of the staff of the botanical section of the Argentine Department of Agriculture.

THE FOLLOWING RESOLUTION was adopted by section G of the A. A. A. S. at the recent Denver meeting:

Resolved: That it is the sense of this section that it would be advisable to establish a research laboratory in connection with the proposed agricultural experiment station in Porto Rico by the Department of Agriculture. Such a laboratory would offer most valuable opportunities for the prosecution of investigations in nearly all branches of botanical science, and would do much to supplement the facilities already offered by American institutions. Extended economic experiments in the tropics must rest more or less directly upon purely botanical research, and the establishment of such a laboratory would do much to strengthen the efficiency of the experiment station. This resolution is not to be taken to mean that the research station should be placed in the same building or buildings with the experiment station, but should be located at the point most favorable for the work in question.

DR. CHARLES MOHR, the venerable botanist, for many years a resident of Mobile, Alabama, died at his home at Asheville, N. C., on July 17. Dr. Mohr was for some years a special agent of the Forestry Division of the U. S. Department of Agriculture, for which he prepared a monograph on *The timber pines of the southern United States*, published in 1896. His most recent work is *Plant life of Alabama*, the result of exploration and study of

the flora for forty years. This volume, which has been nearly three years in the government press, was issued on July 31, unhappily too late for the author to see the full fruition of his labors. This work we shall review later. We learn from *Science* that he had in preparation a volume on the economic botany of Alabama, which is probably too incomplete for publication. He published some years ago a pamphlet on the *Botanical resources of Alabama*.

THE FOLLOWING PAPERS were read before the Botanical Society of America at the recent Denver meeting: J. C. ARTHUR, Clues to relationship among heteroecious plant rusts; W. J. BEAL, Some of the changes now taking place in a forest of oak openings; C. E. BESSEY, Early winter colors of plant formations upon the great plains; E. G. BRITTON and A. TAYLOR, The life history of *Vittaria lineata*; F. E. CLEMENTS, The fundamental phenomena of vegetation, The plant formations of the Rocky mountains (with lantern slides), and A system of nomenclature for phytogeography; W. A. MURRILL (by invitation), The anatomy of the embryo and seedling of *Tsuga Canadensis*; B. L. ROBINSON (address of retiring president), Problems and possibilities of systematic botany; WM. TRELEASE, A suggested hybrid origin of *Yucca gloriosa* (with lantern slides).

The officers elected for the ensuing year are J. C. ARTHUR, *president*; B. T. GALLOWAY, *vice president*; D. T. MACDOUGAL, *secretary*; A. HOLLICK, *treasurer*; C. E. BESSEY and WM. TRELEASE, *councilors*.

THE FOLLOWING PAPERS were read before section G of the A. A. A. S. at the recent Denver meeting: W. J. BEAL, Lantern views of the Botanical garden at the Agricultural college of Michigan; C. E. BESSEY, The morphology of the pine cone; ALICE EASTWOOD, General botanical features of the Coast mountains of California; B. D. HALSTED, Notes upon colors of salsify hybrids; A. C. LEWIS, Contribution to the knowledge of the physiology of karyokinesis; D. T. MACDOUGAL, Thermal relations of plants, and Comparative climate of a meadow and a hemlock forest; AVEN NELSON, Some aspects of the Wyoming desert flora; L. H. PAMMEL, The xerophytic vegetation of the Uintah mountains; F. RAMALEY, Observations on *Egregia Menziesii*, and the plants of the eastern foothills (with lantern slides); A. D. SELBY, Experiments with lime and solutions of formaldehyde in the prevention of onion smut, and germination of seeds of some common cultivated plants after prolonged immersion in liquid air; E. E. SLOSSON, Effect of salt solutions on seeds and plants; WM. TRELEASE, Some protective leaf movements induced by winter temperature (with lantern slides); L. M. UNDERWOOD, The location of a tropical research station in Porto Rico; V. S. WHITE, The Tylostomaceae of North America.

The officers elected for the ensuing year are D. H. CAMPBELL, *vice president*; and H. VON SCHRENK, *secretary*.